Seventh Edition

Biological Anthropology

Michael Alan Park

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Park

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BIOLOGICAL ANTHROPOLOGY

SEVENTH EDITION

MICHAEL ALAN PARK

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BIOLOGICAL ANTHROPOLOGY, SEVENTH EDITION

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PREFACE

Contemporary biological anthropology is a dauntingly broad field. It studies humans in the same way that zoologists study their subject species—from a perspective that includes *all* aspects of the species' biology and that emphasizes the interrelationships among those aspects. In addition to encompassing the traditional topics of the human fossil record and human biological variation, bioanthropology includes primatology, modern technologies in molecular genetics, human demography, disease and medical issues, development of the individual, life histories, and such applications as forensic anthropology. Bioanthropology also appreciates that our cultural behavior is an integral part of our behavior as a species.

No wonder, then, that I (and others I have spoken to) have had difficulty in covering the entire field in a one-semester course. We have ended up leaving out important aspects (or paying them little more than lip service), or we have sacrificed the sense of bioanthropology as an integrated whole for a rushed and encyclopedic inventory of all the field's current topics.

As modern bioanthropology increased in breadth and complexity over the past several decades, so too did the size and detail of introductory texts. Several are now more than 600 pages long. Attempts to produce shorter introductory texts have consisted of simply cutting out parts of these tomes, resulting in rather uneven, sometimes oddly organized, presentations of the field.

I wrote this text in order to present a diverse scientific field to beginning students. Here are the major assumptions that guided my writing:

- Because this is a text for introductory courses, I have tried to reduce the field to its most basic information. No part of the discipline has been left out; instead, I have achieved brevity by managing the level of detail and including only the information necessary to clearly and accurately convey the basic themes, theories, methods, and facts of bioanthropology.

- The text assumes that students have limited background knowledge of the material and little understanding of what science is and how it works. The text *explains* rather than simply itemizes facts and ideas, and it does so, as much as possible, in a narrative format. A lesson from the study of folklore is that a story is far more easily understood and retained than is a list of facts.
- I want students to feel that they are reading a text written by a real person who has participated in the field. I have tried to achieve a balance between informal and formal styles, and I have not shied away from the occasional colloquialism or personal comment.

FEATURES

I've included a number of features that I hope will make this text a more useful learning tool for students.

- *I use the scientific method as a theme throughout the book to demonstrate the integrity and nature of bioanthropology.* I describe the scientific method and then try to show specifically how scientific reasoning has provided us with knowledge about the topics of bioanthropology. For example, I present extended discussions of bipedalism and the issue of modern human origins by posing questions, suggesting answers, and then testing the logic of and evidence for those answers.
- *The text is organized to help students navigate their way through what is still a fairly hefty amount of information.* To help students feel a little less at sea in the midst of new facts and ideas, I regularly refer back to previous topics and ahead to topics that will be covered. The headings and subheadings I use as signposts are as descriptive as possible (for example, "Natural Selection: The Prime Mover of Evolution").
- *Within chapters, a consistent format helps students better understand material new to them.* Each chapter starts with an **introduction,** which sets the stage and context for what's to come, followed by a series of **questions** that the chapter will answer. Because science proceeds by asking and answering questions, this format is also used within the body of the text. A **Contemporary Reflections** box examines a topical application of each chapter's themes and ideas. **Key terms** are

boldfaced in the text and defined in the margins at their first appearance. Each chapter concludes with a list of key terms and a **summary** that not only recaps the important points of the chapter but also provides some new ideas and thoughts that help put the chapter into context within the whole discipline. Also concluding each chapter are **questions for further thought,** which are designed to help students explore the real-world ramifications of the chapter's topics. And a list of **suggested readings,** made up mostly of nontechnical works, tells interested students where to find more information on the material discussed.

- *Two appendixes* discuss in detail the subjects of protein synthesis and population genetics.
- *Two glossaries, a reference list, and a comprehensive index make information more accessible.* A Glossary of Human and Nonhuman Primates, with pronunciations for each term, defines and describes the taxonomic groups discussed in the text. In addition to the running glossary within chapters, a comprehensive Glossary of Terms appears at the back of the book. The References section contains complete sources for the suggested readings and also lists technical works referred to within the text. The Index helps students access information quickly.
- *The text's visual appeal enhances its readability.* Detailed, colorful charts and drawings, as well as full-color photographs, underscore significant points in the text. Captions for the artwork add information rather than simply label the pictures.

WHAT'S NEW IN THIS EDITION?

- The biggest change is in further streamlining and condensing the material presented throughout the book. As a result, the book is now fourteen chapters long instead of fifteen. No major topic is left out; I have simply managed the amount and level of detail so that readers can more easily get to and understand the basic concepts. What I have trimmed are the asides and extended introductions, detail that is not referred to again, and qualifications or exceptions that are not built on later in the text. This gives instructors the choice of adding in details as they wish, either in class or in other readings. My hope is that students will then come to class having the essential material well in mind to build upon.

- Throughout the text, I have further increased the number of chapter headings and subheadings to help readers navigate their way through the material. These headings reinforce ease of study by also acting as a built-in outline of the chapters.
- In a field where new discoveries are made on a regular basis, and vital new interpretations appear frequently, I have been careful to provide the most up-to-date information in all the chapters. There are almost thirty new bibliographic references, half of which come from 2011.
- Among the most important specific chapter changes and updates are these:
    - Chapter 3, "Evolutionary Genetics," reflects new information in that field, including the importance of epigenetics.
    - Chapter 5, "The Origin of Species and the Shape of Evolution" has a new section, "The Grand Pattern of Evolution," that better explains punctuated equilibrium in its context within an independent theory of macroevolution—in terms beginning students can understand.
    - Chapter 7, "The Primates," simplifies the concept of cladistic taxonomy and has a new section, "Are We Hominids or Hominins?" in which I explain why I am returning to the model that classifies only humans in family Hominidae.
    - Chapter 10, "Evolution of the Early Hominids," suffered from a forest-for-the-trees problem. The sections on *Australopithecus* and *Paranthropus* have been condensed to focus on the data at the level of the genus. Details on the individual fossil forms can be added, if desired, by the instructor. I have updated the map and chart to include *A. sediba*.
    - Chapter 11, " The Evolution of Genus *Homo*," begins with a description of the nature and features of the whole genus. I have condensed detail on the individual proposed species of genus *Homo* and have added a new section about the Denisovans. Most important, I condensed the entirety of previous Chapter 12 on the modern human origins debate into a new section in this chapter, which includes my rationale for the change. I have thoroughly updated the chapter to reflect new finds and dates.
    - Chapter 12, "Evolution and Adaptation in Human Populations," I have updated data on causes of death and HIV/AIDS. There is a

new Contemporary Reflections box, “Are There Jewish Diseases? Are There Black Pharmaceuticals?”

- Chapter 13, “Human Biological Diversity,” includes a rewritten and updated section on the genetic evidence for the nonexistence of biological races and a new section on “Anthropology and the History of Race Studies.”

SUPPLEMENTARY MATERIAL

Visit our Online Learning Center Web site at www.mhhe.com/parkba7e for a variety of resources.

- Resources for instructors include the Instructor’s Manual, with chapter overviews, suggested activities, and key terms; a Computerized Testing Program with multiple-choice and short-answer/essay questions; and chapter-specific PowerPoint lecture slides.
- Biological anthropology is eminently visual. Available to students and instructors on the Online Learning Center Web site are fossil images that make the course more vivid and interactive, reinforcing concepts and content students learn in the course.

ACKNOWLEDGMENTS

Thirty-nine years now since leaving Indiana University, I still feel a profound debt to my first teachers there in bioanthropology, Robert Meier, Paul Jamison, and Georg Neumann. This book, I trust, reflects some of the knowledge and inspiration I received from them.

It was Jan Beatty who first brought me to Mayfield Publishing Company over twenty years ago. She was the sponsoring editor of ten editions of my books before Mayfield joined forces with McGraw-Hill. It is an understatement to say that her knowledge of all aspects of publishing, combined with her understanding of anthropology and the needs (and quirks) of us academic types, has been a major influence on all my written work. Although I consider this book the result of a collaboration of many capable people over the years, it owes its heart (in every way) to Jan.

Thanks to the able staff at McGraw-Hill for once again transforming my ideas and words into an attractive and useful finished product.

They are: Nicole Bridge, developmental editor and; Lisa Bruflodt, project manager.

The manuscript was reviewed by the following people: Mark Griffin, San Francisco State University; Melissa Tallman, Hunter College/Columbia University; Michele Buzon, Purdue University; Jeremy DeSilva, Boston University; Anne Titelbaum, Tulane University. I thank them all for their helpful and insightful contributions. All final content, decisions, and errors are, of course, my own.

TO THE READER

The broad field of biological, or physical, anthropology deals with everything from evolutionary theory to the human fossil record to the identification of human skeletal remains from crime scenes and accidents. A detailed account of this whole field would result in an unwieldy text that would be a tough assignment for a one-semester introductory course, especially if it were assigned in its entirety.

This text is intended to truly be an *introduction* to biological anthropology. It will tell you about the many different kinds of studies bioanthropologists participate in and how they conduct them; you'll also learn about the scientific theories and data they use. All the important aspects of bioanthropology are covered here but with just the essential amount of detail. An understanding of the ideas presented in this book will provide you with the basis for delving more deeply into those areas of bioanthropology that interest you.

A major theme of this book is the scientific method. Biological anthropology is a science, so an understanding of how science works is essential. Because the field of anthropology studies the human species in its entirety, however, the text will examine science as a human endeavor, seeing where it fits in the realm of human knowledge.

HOW TO USE THIS BOOK

Each chapter starts with an **introduction** that sets the stage and context for what's to come, followed by a series of **questions** that the chapter will answer. Because science proceeds by asking and answering questions, this format is also used within the body of the text. **Key terms** are boldfaced and defined in the margins at their first appearance. Each chapter ends with a **summary** that not only recaps the important points of the chapter but also provides some new ideas and thoughts that help put what you have just learned into the context of the whole discipline of bioanthropology. There are also **questions for further thought** that will help you explore some of the real-world ramifications of the chapter's topics. A list of **suggested readings**, made up mostly of nontechnical works, tells you where to find more information on topics of particular interest.

A Glossary of Human and Nonhuman Primates defines taxonomic (scientific) names for species discussed in the text—names such as *Homo sapiens* and *Australopithecus afarensis*—and tells you how to pronounce them. In addition to the running glossary within chapters, a comprehensive Glossary of Terms appears at the back of the book. The References section contains complete citations for the suggested readings and also lists technical works referred to within the text. The Index will help you more quickly access information.

To help you visualize specific fossils, a wealth of images is available on the Online Learning Center Web site at www.mhhe.com/parkba7e. Physical anthropology is eminently visual and these images can help bring the course alive for you. Exercises that will allow you to apply specific bioanthropological concepts are also available on this Web site.

PRACTICAL STUDY TIPS

Most Importantly: Establish Your Own Style and Stick to It.

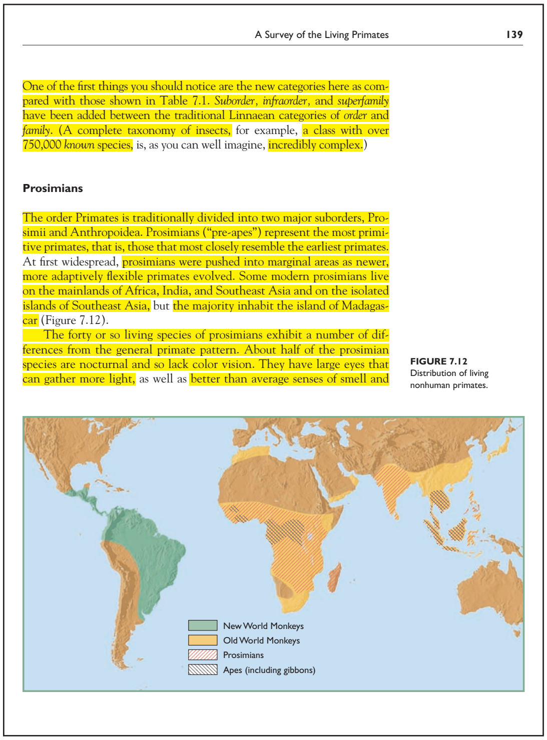
What works for one person won't for another. I always needed peace and quiet to study and still do (and I still *take* courses), but I know some of my students like to study while listening to their iPods. A colleague of mine works with CNN on the TV. Some people highlight passages in the text, others make marginal notes, still others write an outline of the material. Of course, you'll have to adjust your study style to the text in question and to your instructor's format, but for the most part, you can do this around your basic approach. Don't be too inflexible, though; try some of the following suggestions. If they work, fine. If not, forget them.

Read the Text as a Book.

It may sound strange, but this *is* a book. It is not a Web site on paper nor a guide to using other resources. Very simply, it should be read as a *book*, as you would a novel, for example. I wrote it in a "narrative" style. That is, the contents of the chapters and the order of the chapters themselves are meant to convey a story, whereby one idea leads to the next and each idea follows from previous ideas. Stories are how humans have shared information since time immemorial. And because this book is structured as a story—a causal sequence of ideas—it is much easier to retain than is a list of facts.

Don't Highlight Everything.

I've seen some of my students' textbooks with virtually every sentence glowing yellow, pink, or green. This is not helpful, just as it's not helpful to try to write down everything your instructor says in class. Notes and highlighting should be *clues to jog your memory*. Here are two examples—of what not to do and of what would help you actually learn the material:



A Survey of the Living Primates 139

One of the first things you should notice are the new categories here as compared with those shown in Table 7.1. *Suborder*, *infraorder*, and *superfamily* have been added between the traditional Linnaean categories of *order* and *family*. (A complete taxonomy of insects, for example, a class with over 750,000 *known* species, is, as you can well imagine, incredibly complex.)

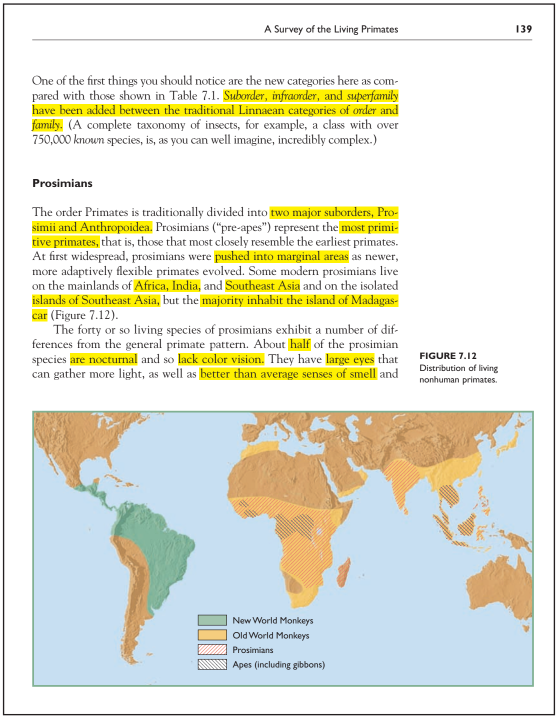
Prosimians

The order Primates is traditionally divided into two major suborders, Prosimii and Anthropoidea. Prosimians ("pre-apes") represent the most primitive primates, that is, those that most closely resemble the earliest primates. At first widespread, prosimians were pushed into marginal areas as newer, more adaptively flexible primates evolved. Some modern prosimians live on the mainlands of Africa, India, and Southeast Asia and on the isolated islands of Southeast Asia, but the majority inhabit the island of Madagascar (Figure 7.12).

The forty or so living species of prosimians exhibit a number of differences from the general primate pattern. About half of the prosimian species are nocturnal and so lack color vision. They have large eyes that can gather more light, as well as better than average senses of smell and

FIGURE 7.12
Distribution of living nonhuman primates.

See the difference?



A Survey of the Living Primates 139

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FIGURE 7.12
Distribution of living nonhuman primates.

Use the Ancillary Material as Support.

The text in the book, with the illustrations and captions, is the main part. The running glossary entries (in the margins), opening questions, material at the ends of chapters, the main glossary, and the Online Learning Center Web site are all there to help you *make sense of and learn* the material in the book. Use all these things to help you define words and test your knowledge of the material, but don't start with them or rely on them. The text I had when I took introductory anthropology had *none* of these things. They are helpful but not necessary.

Organize Reviewing and Studying for Exams.

For this book, I'd suggest first rereading the opening questions and then the summary for each chapter. These will remind you of the themes of the chapter, the general ideas that the facts are supporting. Then, review your highlights and notes. Finally, see if you can answer the opening questions.

Ask Questions!

If you miss one idea, you may well miss many ideas that follow from it. Write down questions that occur to you, or make notes in the margins of the book. Then get answers to them as soon as you can. And while it's a cliché, it's true: No question is stupid. Someone else in the class may well have the same question. And if you would like my input, feel free to email me at: ParkM@ccsu.edu.

BIOLOGICAL ANTHROPOLOGY

1

CHAPTER

Biological Anthropology

Anthropologists study spiders, right?
—Anonymous Caller

If you asked twenty people to define anthropology, you would probably get twenty different answers. Anthropology is such a broad field that many people, understandably, are not sure just what an anthropologist studies.

In this chapter, we will define anthropology in general and then focus on the subfield of biological anthropology (also called *bioanthropology* or *physical anthropology*). Because fieldwork is perhaps the best-known aspect of anthropology and is the part that attracts many students to the discipline, I will begin with a brief description of two of my experiences.

As you read, consider the following questions:

What is anthropology, and what are its subfields?

What is biological anthropology?

How does the scientific method operate?

In what way is bioanthropology a science?

IN THE FIELD: DOING BIOLOGICAL ANTHROPOLOGY

Among the Hutterites

The wheat fields on either side of the long, straight road in western Saskatchewan, Canada, stretched as far as the eye could see. I found myself wishing, on that June day in 1973, that the road went on just as far. I was on my way to visit with my first real anthropological subjects, a colony of people belonging to a 475-year-old religious denomination called the Hutterian Brethren, or Hutterites.

Up to this point, I had not felt much anxiety about the visit. Accounts by other anthropologists of their contacts with Amazon jungle warriors and New Guinea headhunters made my situation seem rather safe. The Hutterites are, after all, people who share my European American cultural heritage, speak English (among other languages), and practice a form of Christianity that emphasizes pacifism and tolerance.

At this point, though, those considerations, no matter how reassuring they should have been, didn't help. I simply had that unnamed fear that affects nearly all anthropologists under these first-contact circumstances.

Finally, the road turned from blacktop to dirt, curved abruptly to the right and crested a hill, and I saw below a neat collection of twenty or so white buildings surrounded by acres of cultivated fields. This was the Hutterite colony, or *Bruderhof*, the "place where the brethren live" (Figure 1.1).

As we drove into the colony, not a soul was in sight. My companion explained that it was a religious holiday that required all but essential work to cease. Everyone was indoors observing the holiday, but the colony minister and colony boss had agreed to see me.

I entered one of the smaller buildings. The interior was darkened, in keeping with the holiday. A few minutes later, having gotten my bearings, I explained the reason for my visit to two men and a woman.

The men were dressed in the Hutterite fashion—black trousers and coats and white shirts—and they wore beards, a sign of marriage. The older, gray-haired man was the colony minister. The younger man, who happened to be his son, was the colony boss. The woman, the minister's wife, also dressed in the conservative style of the Hutterites and related groups. She wore a dress with a white blouse underneath. Her head was covered by a polka-dot kerchief, or *shawl* (Figure 1.2).

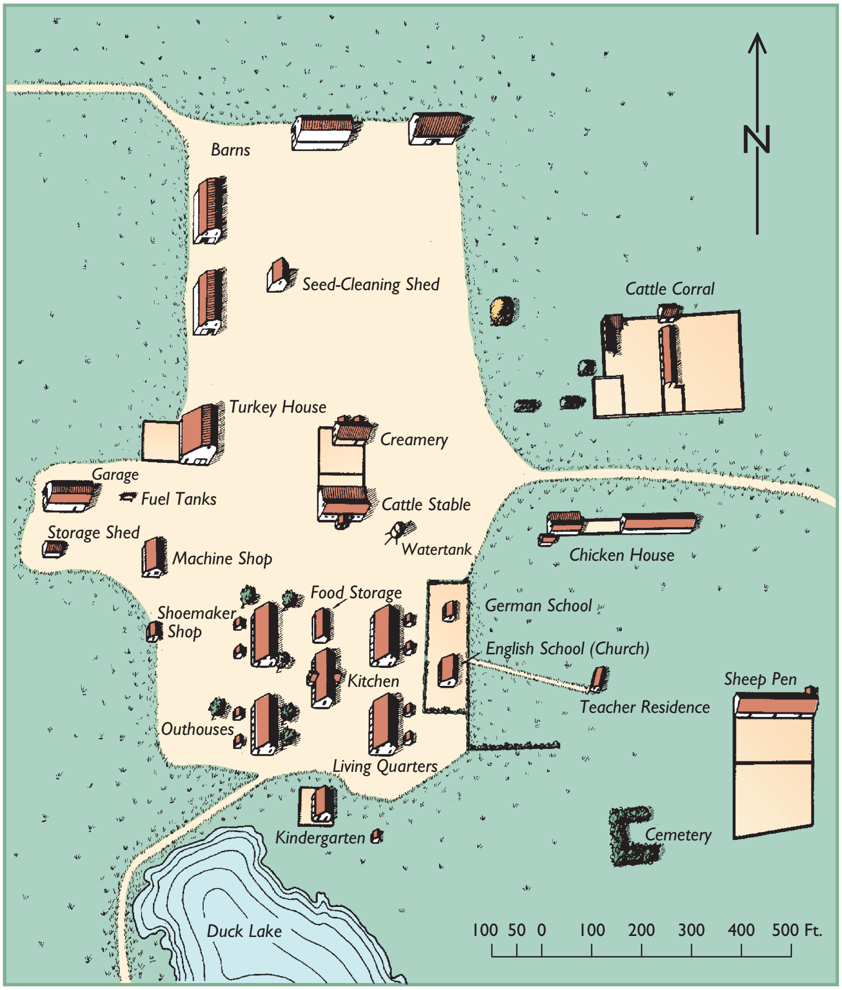
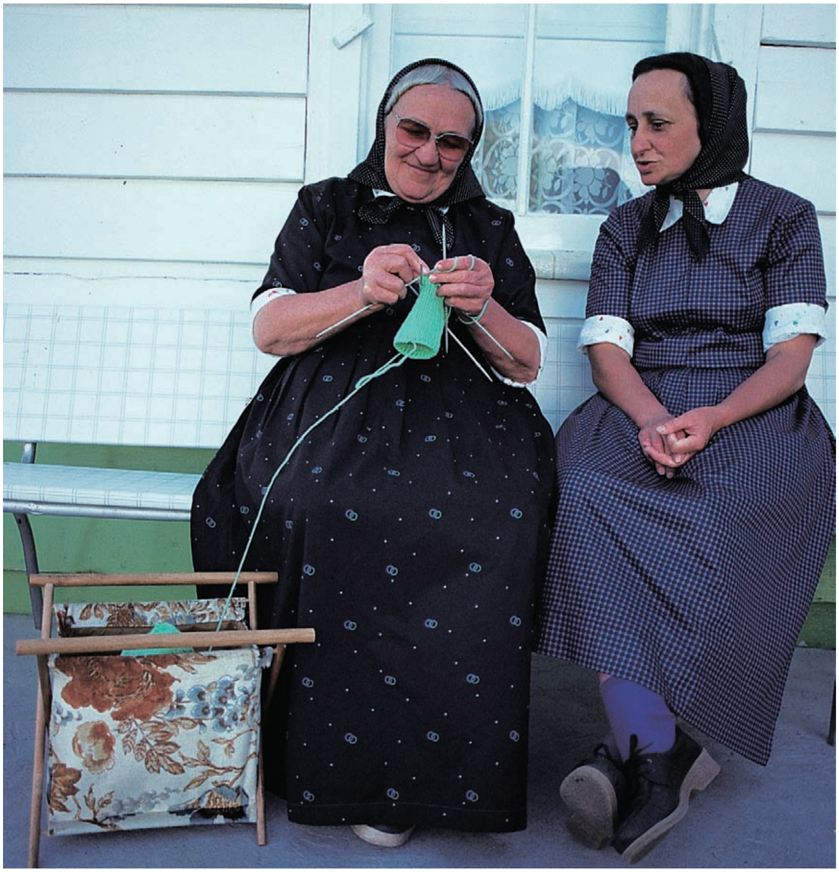

N
Barns
Seed-Cleaning Shed
Cattle Corral
Turkey House
Creamery
Garage
Fuel Tanks
Cattle Stable
Storage Shed
Machine Shop
Watertank
Chicken House
Food Storage
Shoemaker Shop
German School
English School (Church)
Kitchen
Sheep Pen
Teacher Residence
Outhouses
Living Quarters
Kindergarten
Cemetery
Duck Lake
100 50 0 100 200 300 400 500 Ft.

FIGURE 1.1
Diagram of a typical Hutterite colony. The variety of buildings and their functions are indicative of the Hutterites' attempt to keep their colonies self-sufficient and separate from the outside world.

My visit had been arranged and the Hutterites had an idea of what I wanted to do. But if the colony members didn't like me or my planned study, they could still decline to cooperate. The three listened in silence as I went through my well-rehearsed explanation. When I had finished, they asked me only a few questions, such as: Was I from the government? (My study involved using fingerprints as hereditary traits—a now outdated method—and they apparently associated fingerprinting with law enforcement and personal identification.) What would I use this study for? Was I going to write a book?

FIGURE 1.2
Hutterite women in typical dress.



I expected them to confer with one another or ask me to come back when they had decided if they would allow me to conduct the study. Instead, the minister, who was clearly in charge, simply said, “Today is a holiday for us. Can you start tomorrow?”

And so, for the next month I took part in my personal version of fieldwork—taking fingerprints, recording family relationships, observing colony life, and getting to know the Hutterites of this and one other Canadian Bruderhof (Park 1979; Figure 1.3).

What exactly had brought me 1,300 miles from my university to the northern plains, to this isolated community of people whose way of life has changed little over the past 475 years and whose lifestyle and philosophy differ so much from those of North Americans in general? Essentially, it

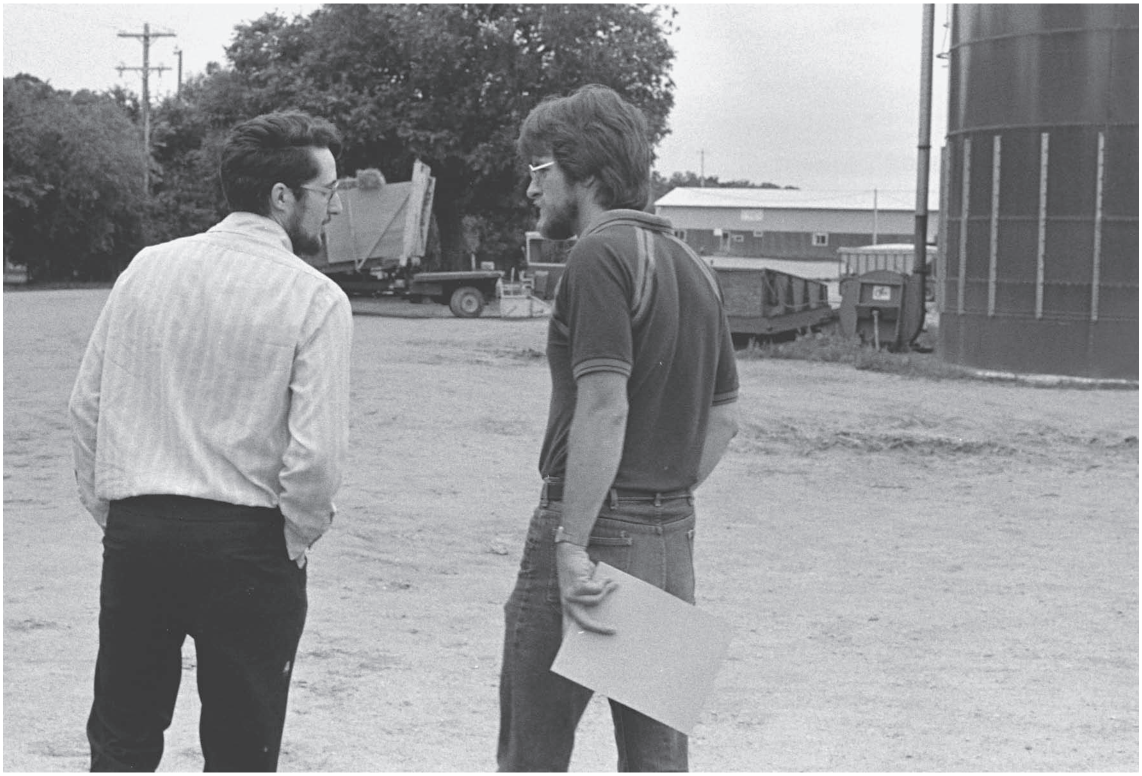


FIGURE 1.3
Author (*right*) and Hutterite informant. I already had the beard, but it was suggested that I keep it so that I would look more familiar to the Hutterite children.

was the same thing that takes anthropologists to such locations as the highlands of New Guinea, the caves of the Pyrenees, and the street corners of New York City: the desire to learn something about the nature of the human species. In my case, I was pursuing an interest I had developed early in graduate school—to study the processes of evolution and how they affect humans. I was curious about two of these processes: gene flow and genetic drift (see Chapter 4 for details).

To examine the actions of these processes on human populations and to determine their roles in human evolution, I needed to find a human group with a few special characteristics. The group had to (1) be genetically isolated, (2) be fairly small as a whole but with large families, and (3) consist of individual populations that resulted from the splitting of earlier populations.

The Hutterites exhibited all these characteristics. I discovered them through library research on genetically isolated groups. My opportunity to study them was greatly enhanced by a stroke of luck. A fellow graduate student was the daughter of a local wheat farmer and his wife who became my "public relations advisors."

A Hawaiian in Connecticut

Exactly twenty years after my fieldwork with the Hutterites, I found myself standing over an open grave in an old cemetery in the wooded hills of northwest Connecticut. Our team of anthropologists was hoping to find the remains of a native Hawaiian who had been buried here in 1818 and who was now, after 175 years, going home.

A few weeks earlier, Nick Bellantoni, the Connecticut State Archaeologist (and a former student of mine), had called me with a fascinating story. In 1808 a young Hawaiian named Opukaha'ia (pronounced *oh-poo-kah-hah-ee'-ah*) escaped the tribal warfare that had killed his family by swimming out to a Yankee whaling vessel, where he was taken on board as a cabin boy. Two years later, he ended up at Yale University in New Haven, Connecticut. He took the name Henry, converted to Christianity, and became a Congregational minister who helped build a missionary school in Cornwall, Connecticut. His dream was to return to Hawaii and to take his new faith to the people there (see his portrait in Figure 1.6).

Sadly, Henry's dream was never realized. He died in a typhoid epidemic in 1818 at the age of 26, but his vision inspired the missionary movement that was to change the history of the Hawaiian Islands forever. His grave in Cornwall became a shrine both for the people of his adopted land and for visiting Hawaiians, who would leave offerings atop his platform-style headstone (Figure 1.4).

Nearly two centuries after his death, a living relative of Henry's had a dream that she would honor Henry's final wish to return to his native land. After almost a year of raising funds and making the necessary arrangements, her dream was to come true. And this is where anthropology comes in.

Old New England cemeteries tended to be inexact in the placement of headstones relative to the bodies buried beneath them, and the acidic New England soil is unkind to organic remains. Both logically and legally, this was a job for the state archaeologist, and Nick wanted my help in recovering and identifying whatever remains we might be lucky enough to find.

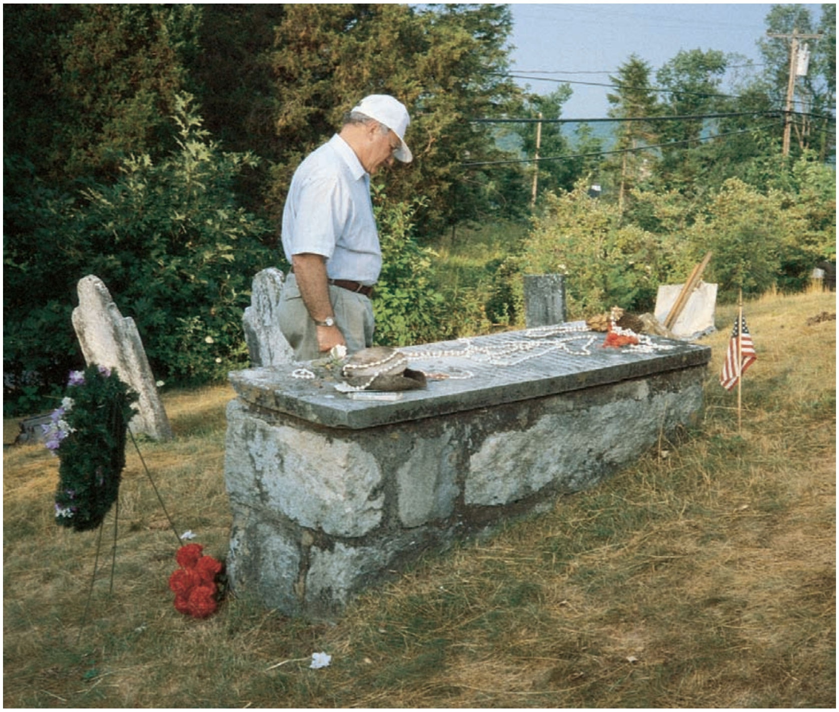


FIGURE 1.4
Grave of Henry Opukaha‘ia with offerings left by visitors.

We dismantled the pedestal with care, labeling each stone and diagramming its position, since it was to be rebuilt in Hawaii by a stonemason. Under the pedestal and going down about 3 feet into the ground, we uncovered three more layers of fieldstone, which acted as a foundation for the monument and protection for the coffin and the remains we hoped were still below. When all the stones had been removed and we were into a layer of sandy soil, Nick worked alone, delicately scraping away the dirt inch by inch (Figure 1.5).

Late on the second day of our excavation, the remnants of the coffin came into view. In fact, the wooden coffin itself had long since decayed. All that was left was the dark stain of its outline in the soil. We began to despair of finding much else, but an hour later Nick's trowel grazed something hard, and in a few minutes the apparent remains of Henry Opukaha‘ia saw the light of day for the first time in 175 years.

We soon learned that the skeleton was virtually complete. But was it *Henry*? As Nick slowly freed each bone from the soil and handed it up to

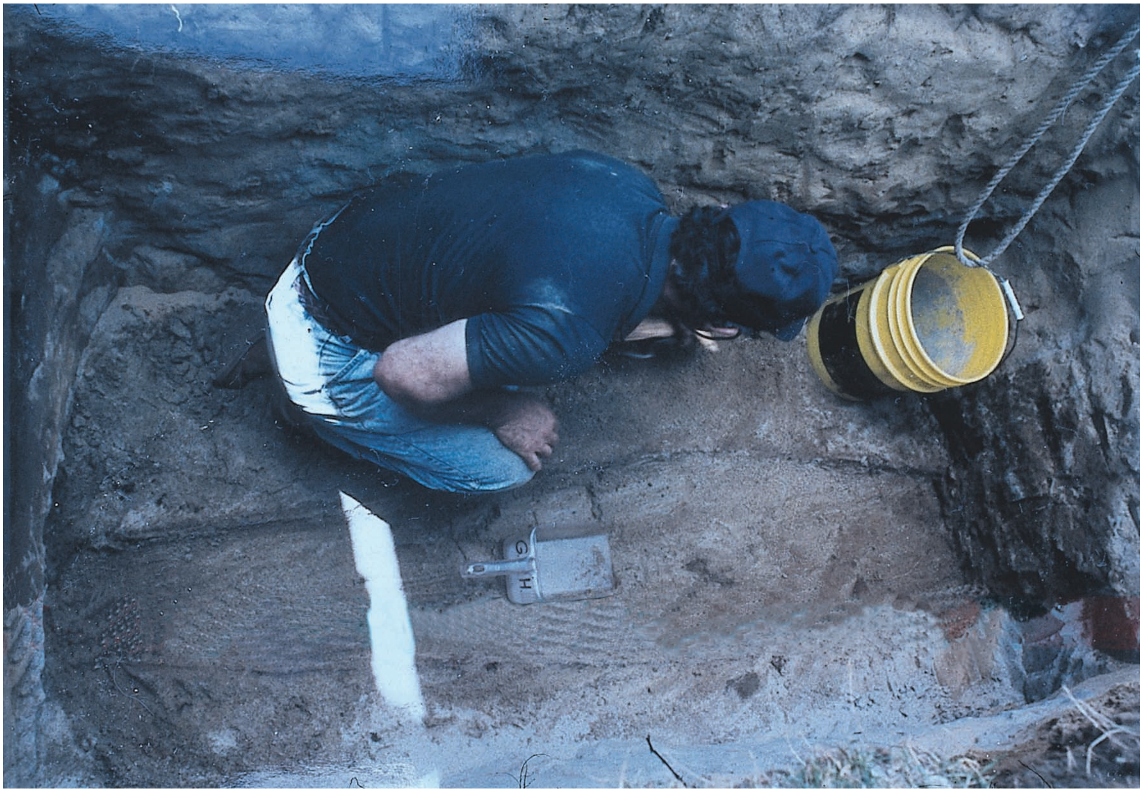


FIGURE 1.5
Nick Bellantoni excavating the grave of Henry Opukahaʻia. The pattern on the floor of the excavation marks the coffin outline.

me (see chapter-opener photograph), we recorded it and compared it with what we knew of Henry from written descriptions and a single portrait. The skeleton was clearly that of a male and, at first glance, conformed to that of a person in his late 20s of about the right size. Henry had been described as being "a little under 6 feet," and the long bones of the arms and legs confirmed this. The skull, however, confirmed our identification. As the dirt was brushed away, the face of Henry Opukahaʻia emerged, the very image of his portrait. (The family has requested that, for religious reasons, photographs of Henry's remains not be published.)

We spent two more days with the bones, cleaning, photographing, measuring, and describing each. Finally, we placed each bone in its proper anatomical position in spaces cut into heavy foam rubber that lined the bottom of a *koa*-wood coffin, specially made and shipped from Hawaii. The following Sunday, we attended a memorial service in Cornwall, and then Henry's remains began their long journey back home (Figure 1.6).

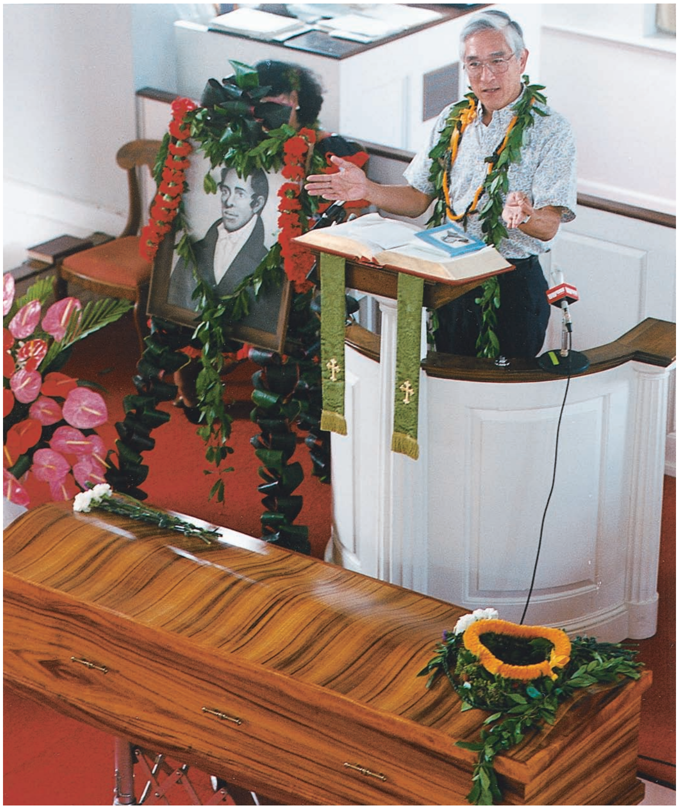


FIGURE 1.6
Reverend David Hirano, from Hawaii, speaks over the remains of Henry Opukahaʻia at his "homegoing" celebration in Cornwall, Connecticut. The *koa*-wood coffin, *ti* leaves, and flowered *lei* all have symbolic meaning in Hawaiian culture.

WHAT IS BIOLOGICAL ANTHROPOLOGY?

My experiences as a biological anthropologist range from examining the esoteric detail of evolutionary theory to using my knowledge of the human skeleton for a very personal endeavor. These are just two examples of the many things that biological anthropologists do.

Defining Anthropology

Biological anthropology (or **bioanthropology** or **physical anthropology**) needs to be defined within the context of anthropology as a whole. **Anthropology,** in general, is defined as the study of the human **species.**

biological anthropology	A subfield of anthropology that studies humans as a biocultural species.
bioanthropology	Another name for biological anthropology.
physical anthropology	The traditional name for biological anthropology.
anthropology	The biocultural study of the human species.
species	A group of organisms that can produce fertile offspring among themselves but not with members of other groups.

Anthropologists study the human species as any zoologist would study an animal species. We look into every aspect of the biology of our subject—genetics, anatomy, physiology, behavior, environment, adaptations, and evolutionary history—stressing the interrelationships among these aspects.

This **holistic** approach is the hallmark of anthropology. We understand that all the facets of our species—our biology, our behavior, our past, and our present—interact to make us what we are.

But here's where it gets complicated. The most characteristic feature of our species' behavior is **culture,** and cultural behavior is not programmed in our genes, as is, for example, much of the behavior of other species. Human culture is learned. We have a biological potential for cultural behavior in general, but exactly *how* we behave comes to us through all our experiences. Take language, for example. All humans are born with the ability to learn a language, but it is the language spoken by our respective families and our broader cultures that determines what language we will speak.

Moreover, cultural knowledge involves not just specific facts but also ideas, concepts, generalizations, and abstractions. You were able to speak your native language fairly fluently before you were ever formally taught the particulars of its grammar. You did this by making your own generalizations from the raw data you heard and the rules they followed, from the speech of others and from trying to make yourself understood. Even now when you speak, you are applying those generalizations to new situations. And each situation—every conversation you have, every essay you write, every book you read—is a new situation.

In addition, because culture exists in the context of human social interactions, it must be shared among members of a social group. The complexity of cultural ideas requires this sharing to involve symbols—agreed-upon representations of concepts and abstractions. Human language, of course, is symbolic, as are many visual aspects of our cultures.

In short, culture is highly variable and flexible. It differs from society to society, from environment to environment, and from one time period to another. It even differs in its details from one individual to another. We continually modify our cultural behaviors to fit the unique circumstances of our lives.

So another characteristic of the field of anthropology is its **biocultural** approach. Anthropology seeks to describe and explain the interactions between our nature as a biological species and the cultural behavior that is our species' most striking and important trait. We will encounter many examples of these interactions as we continue.

holistic Assuming an interrelationship among the parts of a subject.

culture Ideas and behaviors that are learned and shared. Nonbiological means of adaptation.

biocultural Focusing on the interaction of biology and culture.

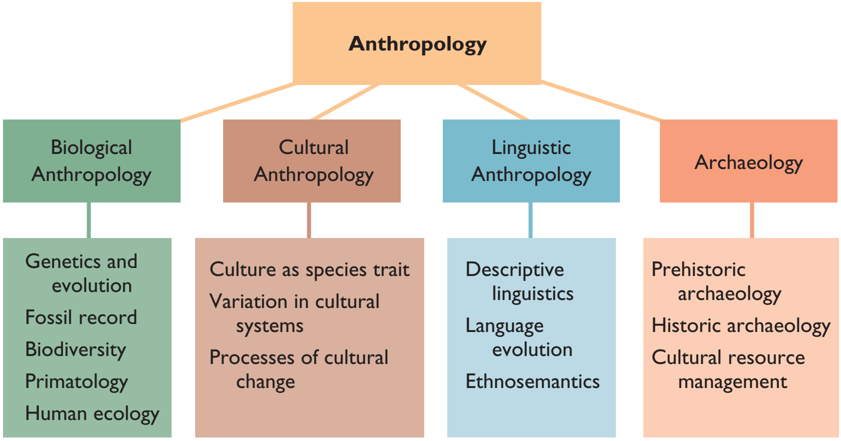

Anthropology
Biological Anthropology
Cultural Anthropology
Linguistic Anthropology
Archaeology
Genetics and evolution
Fossil record
Biodiversity
Primatology
Human ecology
Culture as species trait
Variation in cultural systems
Processes of cultural change
Descriptive linguistics
Language evolution
Ethnosemantics
Prehistoric archaeology
Historic archaeology
Cultural resource management

FIGURE 1.7
Major subfields of anthropology with some of their topics. The topics of each subfield may be applied to various social issues (see Chapter 14); this is collectively called *applied anthropology*.

All these different dimensions make the study of the human species complex and challenging, and so anthropology, the discipline that takes on this challenge, is typically divided into a number of subfields (Figure 1.7). Biological anthropology looks at our species from a biological point of view. This includes all the topics covered in this book. **Cultural anthropology** is the study of culture as a characteristic of our species and of the variation in cultural expression among human groups. This includes human language, although sometimes **linguistic anthropology** is considered a separate subfield. **Archaeology** is the study of the human cultural past and the reconstruction of past cultural systems. It also involves the techniques used to recover, preserve, and interpret the material remains of the past. The theoretical basis for these activities is the study of the relationship of material culture with cultural systems as a whole.

cultural anthropology A subfield of anthropology that focuses on human cultural behavior and cultural systems and the variation in cultural expression among human groups.

linguistic anthropology A subfield of anthropology that studies language as a human characteristic and attempts to explain the differences among languages and the relationship between a language and the society that uses it.

archaeology A subfield of anthropology that studies the human cultural past and the reconstruction of past cultural systems.

The Specialties of Bioanthropology

The specialties of biological anthropology are best expressed in terms of the questions we seek to answer about human biology:

1. What are the biological characteristics that define the human species? How do our genes code for these characteristics? Just how much do genes contribute to our traits? How much are traits shaped by the environment? How does evolution work, and how does it apply to us? (These were the questions I was pursuing in my study of the Hutterites.)

2. What is the physical record of our evolution? This is the specialty referred to as **paleoanthropology,** the study of human fossils based on our knowledge of skeletal biology, or **osteology.**
3. What sort of biological diversity do we see in our species today? How did it evolve? What do the variable traits mean for other aspects of our lives? What do they *not* mean?
4. What can we learn about the biology of our close relatives, the nonhuman **primates,** and what can it tell us about ourselves? This specialty is called **primatology.**
5. What do we know about **human ecology,** the relationships between humans and their environments?
6. How can we apply all this knowledge to matters of current concern? This is often called **applied anthropology** and can refer to all the subfields. (The exhumation of Henry Opukaha'ia is an example.)

We'll discuss these studies, and many more, as we survey the field of bioanthropology. As we do, keep in mind that what connects these varied activities is their focus on *learning about human beings as a biocultural species*.

The specialties of bioanthropology are also connected in that they are all scientific. In many cases, they may not seem to fit the common conception of science. Most anthropologists don't wear white lab coats or work with test tubes and chemicals. Many anthropologists study things that can't be directly observed in nature or re-created in the lab because they happened in the past. But bioanthropology *is* a science, just as much as chemistry, physics, and biology.

paleoanthropology A specialty that studies the human fossil record.

osteology The study of the structure, function, and evolution of the skeleton.

primates Large-brained, mostly tree-dwelling mammals with three-dimensional color vision and grasping hands. Humans are primates.

primatology A specialty that studies nonhuman primates.

human ecology A specialty that studies the relationships between humans and their environments.

applied anthropology Anthropology used to address current practical problems and concerns.

science The method of inquiry that requires the generation, testing, and acceptance or rejection of hypotheses.

theory A well-supported general idea that explains a large set of factual patterns and predicts other patterns.

scientific method The process of conducting scientific inquiry.

BIOANTHROPOLOGY AND SCIENCE

The goal of **science** is to relate and unify facts in order to generate an accurate description of the world and, eventually, broad principles known as **theories.** But how does science work?

The Scientific Method

The most basic step of the scientific method is asking the questions we wish to answer or describing the observations we wish to explain. We then look for patterns, connections, and associations so that we can generate educated guesses as to possible explanations. These educated guesses are called **hypotheses.** In other words, we try to formulate a *general* explanatory principle that will account for the *specific* pieces of real data we have observed and want to explain. This process of reasoning is called **induction.**

Next comes the defining characteristic of science. We must attempt to either support or refute our hypothesis by testing it. Tests may take many forms, depending on what we are trying to explain, but basically we reverse the process of induction and go from the general back to the specific by making predictions: *If* our general hypothesis is correct, *then* what other specific things should we observe? This process is called **deduction.** For example, we look for

> *Repetition:* Does the same phenomenon occur over and over?
>
> *Universality:* Does the phenomenon occur under all conditions? If we vary some aspect of the situation, will the phenomenon still occur? How might different situations change the phenomenon?
>
> *Explanations for exceptions:* Can we account for cases where the phenomenon doesn't appear to occur?
>
> *New data:* Does new information support or contradict our hypothesis?

If we find one piece of evidence that conclusively refutes our hypothesis, the hypothesis is disproved, at least for the moment. But if a hypothesis passes every test we put it to, we use it as a basis for further induction and testing. Notice that I didn't say we *prove* a hypothesis. Good science is skeptical, always looking for new evidence, always open to and, indeed, inviting change. The best we should honestly say about most hypotheses is that, so far, no evidence has been found that *disproves* them.

When, through this process, we have generated an integrated body of ideas, we have a theory. In science, *theory* is a positive term. Theories are called *theories* because they are general ideas that explain a large number of phenomena and are themselves made up of interacting and well-supported hypotheses. All the facts of biology, for instance, make sense within the general theory of evolution—that all life has a common ancestry and that living forms change over time and give rise to new forms by various natural processes.

hypotheses Educated guesses to explain natural phenomena.

induction Developing a general explanation from specific observations.

deduction Suggesting specific data that would be found if a hypothesis were true.

Some Common Misconceptions about Science

A theory is not the end of the scientific method. No theory is complete. For example, some force we call *gravity* exists, but we still don't understand how gravity works and how it originated and separated from the other

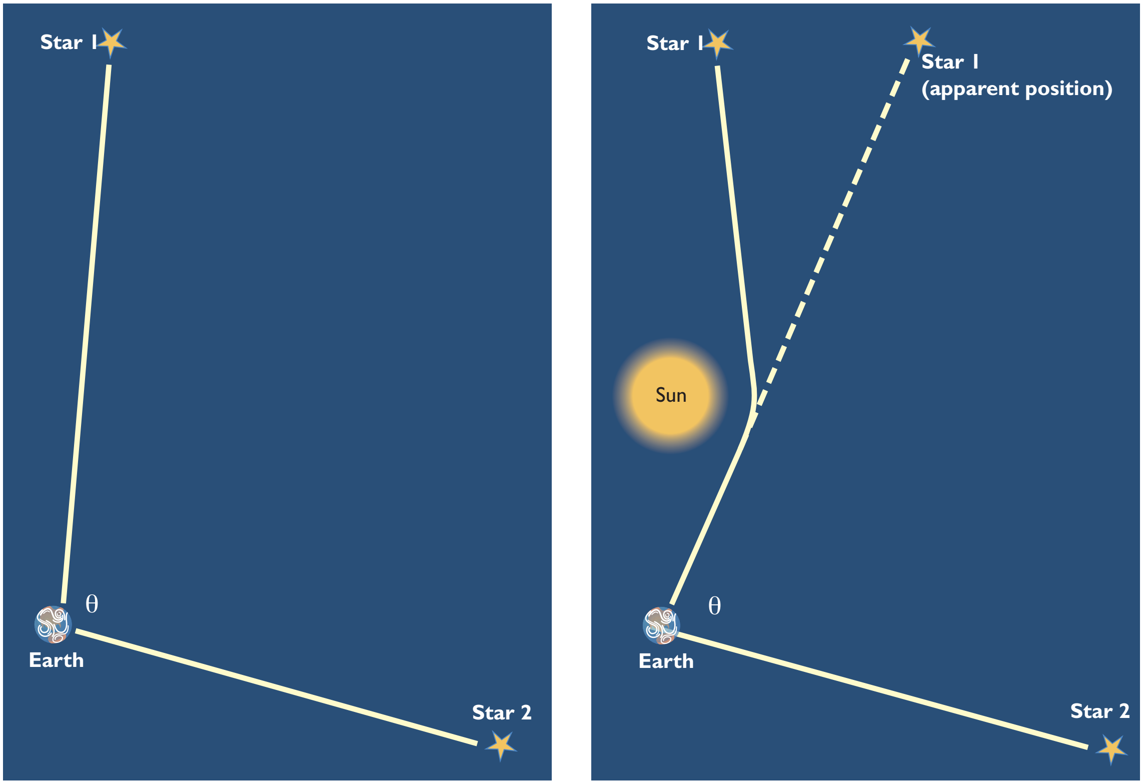


FIGURE 1.8
Light bent by gravity. Einstein predicted in 1905 that a strong gravitational field could bend light. His prediction was verified in 1919, when light from stars that should have been blocked by the sun could be seen during a solar eclipse. The effect is greatly exaggerated in these drawings.

forces of nature. In other words, we still have hypotheses to test to arrive at a complete theory of gravity.

Another popular misconception about science is that it studies only visible, tangible, present-day things—chemicals, living organisms, planets and stars. But notice that gravity is neither visible nor tangible. We know it exists because all our deductive predictions support its existence. We see gravity at work from the levels of our everyday lives to that of the entire universe (Figure 1.8). We can even explain exceptions *within the context of our general idea*. The reason a helium-filled balloon seems to violate gravity can be explained by the existing theory of gravity: helium is less dense than the surrounding air and so responds relatively less to the earth's gravity, floating on the air as a boat floats on water.

Similarly, past events can't be seen or touched. They can't be experimented on directly or repeated exactly. The evolution of plants and animals is an example. But again, we know that evolution occurs because the theory has passed all our tests. The theory of evolution explains observations of the real world. We have observed everything we predicted we would *if* evolution occurred. (We'll look more closely at how science has generated and supported the theory of evolution in Chapter 2.)

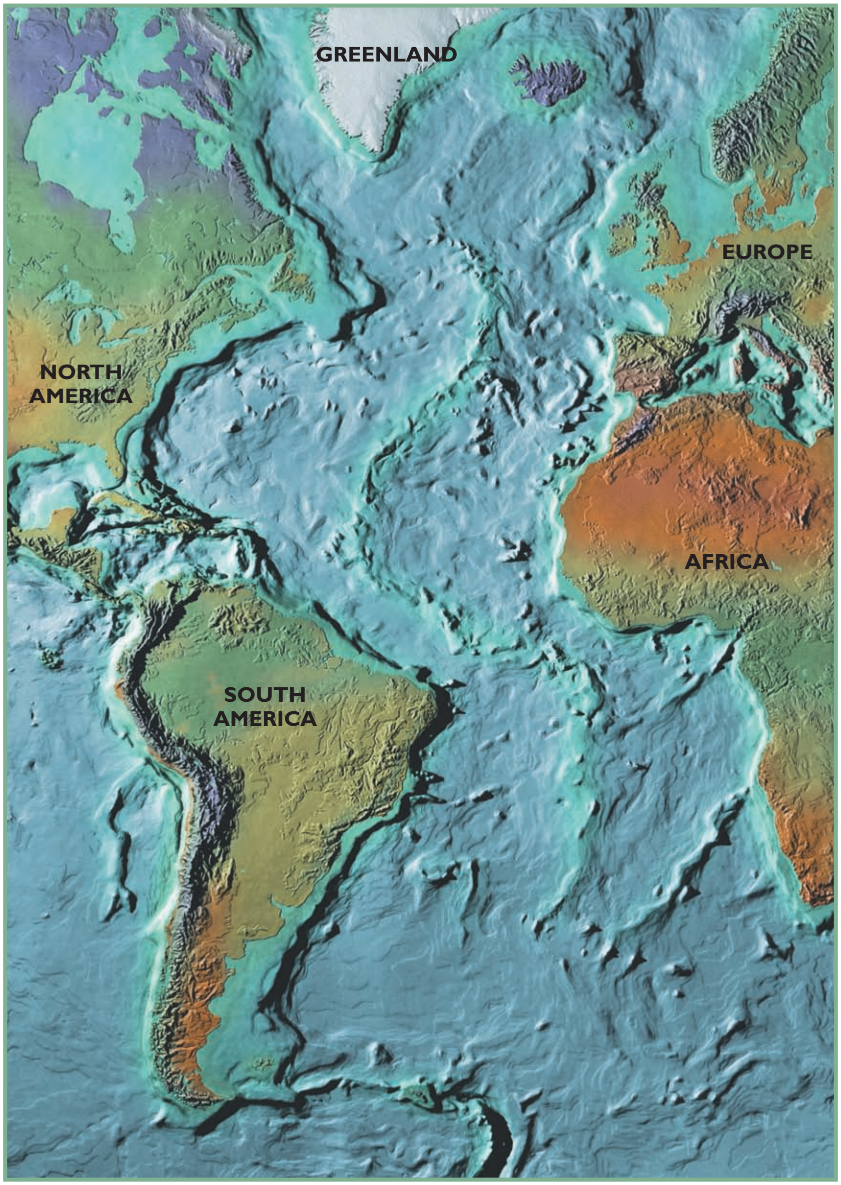
Science Is Conducted in a Cultural Context

We must acknowledge that scientists are members of their societies and participants in their cultures. Thus, science—as objective as we try to make it—is always constrained by what we already know, by what we still don't know, by the technology available to us to gather and test data, by existing theories, and even by certain influential social or cultural trends.

For example, I remember back in the mid-1950s, when one of my elementary school teachers pointed out that the east coast of South America and the west coast of Africa seemed to potentially fit together like a giant jigsaw puzzle (Figure 1.9). Of course, she had said, there's no way the continents could move around, so it must just be a coincidence. In fact, she was reflecting our scientific knowledge of the time. There was plenty of geological and fossil evidence suggesting that the continents had moved around, but although the idea of continental drift had been proposed in 1912, there was no mechanism to explain it. Beginning in the 1960s, however, new technologies gave us new evidence that provided such a mechanism. We now have a well-verified theory of continental drift by the process of plate tectonics (see Chapter 6).

An interesting example of an influential social trend comes from a hypothesized explanation for the famous Salem witch trials in Massachusetts in 1692, when a group of young girls accused some adults of witchcraft, with the result that twenty people were executed. The hypothesis suggested that the people of Salem had consumed bread made from grains tainted with ergot, a fungus that contains alkaloids, some of which are derivatives of lysergic acid, which in turn is used in the synthesis of the hallucinogenic drug LSD. In other words, maybe the young girls who made the witchcraft accusations were inadvertently having an "acid trip." Not surprisingly, this explanation arose and found popularity in the 1960s, a period associated in part with the so-called drug culture. Although the idea showed up recently in a public-television documentary, there is no evidence to support it.

FIGURE 1.9
Topographic map of the Atlantic Ocean floor showing the correlating outlines of the edges of the Eastern and Western Hemispheres. Also shown is the Mid-Atlantic Ridge—evidence for the plate tectonics that pushed the once-connected continents apart.



These examples show us why scientific skepticism is so important and why we should actively question and re-examine even our most well-supported ideas. Science answers questions about our lives and about the world in which we live. For an answer to be accepted scientifically, it must pass all tests and be refuted by none.

Contemporary Reflections

Is Evolution a Fact, a Theory, or Just a Hypothesis?

It may surprise you that the answer is "all of the above." Evolution, as a broad topic, incorporates theory, fact, *and* hypothesis. This is because the scientific method is not a nice, neat, linear series of steps from first observation to final all-encompassing theory. Rather, science works in a cycle, and the inductive and deductive reasoning of science is applied constantly to the different aspects of the same general subject. Data and hypotheses are always being re-examined, and each theory itself becomes a new observation to be questioned, tested, explained, and possibly changed.

A theory is a well-supported idea that explains a set of observed phenomena. Evolution is a theory in that all our observations of life on earth—fossils, the geological formations in which they are found, and the biology of living creatures—make sense and find explanation within the concept of evolution, the idea that living things change through time and that organisms are related as in a huge branching tree, with existing species giving rise to new species.

There is so much evidence in support of evolution that this tried-and-tested theory may reasonably be considered a fact. A good analogy is the accepted fact that the earth revolves around the sun and not, as people thought for so long, the other way around. But how do we *know* the earth revolves around the sun? It certainly appears upon daily observation to do just the opposite. We accept the heliocentric (sun-centered) theory because there is so much data in its support. It makes so much sense and explains so many other phenomena that we consider it a fact and take it for granted, never giving it much thought on a regular basis. I would be very surprised to read in tomorrow's newspaper that some new evidence refuted the idea. Similarly, that evolution occurs and accounts for the nature of life on earth is, for all intents and purposes, a fact.

But that fact poses more questions. A big one (the one that confronted Darwin) is *how* evolution takes place. The fact of evolution now becomes a new observation that requires explanation through the generation of new hypotheses and the subsequent testing and retesting of those hypotheses. Darwin proposed a mechanism he called *natural selection* and then, over many years, examined this hypothesis against real-world data. The mechanism of natural selection is now so well supported that we call it, too, a fact.

But an overall explanation for how evolution works—a theory to explain the observed fact of evolution—is far from complete. We know that mechanisms in addition to natural selection contribute to evolution. The relative importance of all these mechanisms is still being debated. The broad picture of evolution—the "shape" of the family tree of living things—is a matter of much discussion. The specific genetic processes behind all evolutionary change are really only beginning to be revealed as new technologies are letting us look at the very code of life. In other words, we are still examining hypotheses to account for how evolution takes place and for what happened in evolutionary history.

Evolution—like any broad scientific idea—involves a complex and interacting web of facts, hypotheses, and theories. It is the never-ending nature of scientific inquiry that can make science so frustrating—but also so exciting and so important in the modern world.

SUMMARY

Anthropology is the biocultural study of the human species. Cultural anthropology studies human culture, cultural systems, and their variation. Our species' most characteristic feature today is our cultural behavior, which is expressed in a great variety of ways among different societies.

The majority of human cultural systems that ever existed did so in the past and so have left us only meager physical remains of their presence and nature. Archaeology recovers and interprets these remains.

Biological anthropology studies the human species the way biology studies any species, examining our biological characteristics, our evolution, our variation, our relationship with our environment, and our behavior, including our ability to have culture.

Bioanthropology, as a scientific discipline, asks questions about the human species and then attempts to answer them by proposing hypotheses and by testing those hypotheses, looking both for evidence in their support and for anything that would refute them.

QUESTIONS FOR FURTHER THOUGHT

1. Anthropologists have special responsibilities when studying other human beings. What sorts of issues do you think I had to take into account when conducting my research among the Hutterites? What issues would have been involved in the exhumation of Henry Opukaha'ia? Consider another culture you are familiar with, and imagine what particular issues would be involved in studying it as an anthropologist.
2. Because of anthropology's wide scope of interests and its overlap with other scholarly disciplines, anthropologists have sometimes been described as "jacks of all trades and masters of none." How would you respond to this?

KEY TERMS

biological anthropology
bioanthropology
physical anthropology
anthropology
species
holistic
culture
biocultural
cultural anthropology
linguistic anthropology
archaeology
paleoanthropology
osteology
primates
primatology
human ecology
applied anthropology
theory
science
scientific method
hypotheses
induction
deduction

SUGGESTED READINGS

For more personal experiences of biological anthropologists, see part 1 of my *Biological Anthropology: An Introductory Reader*, sixth edition. *(Complete publication details of the suggested readings appear in the "References.")*

For more information on the Hutterites, see John Hostetler's *Hutterite Society*.

For a longer discussion of the nature of science and the scientific method, see Kenneth L. Feder's *Frauds, Myths, and Mysteries: Science and Pseudoscience in Archaeology*, seventh edition, and for even more detail see *Understanding Scientific Reasoning*, by Ronald N. Giere.

The field of anthropology in general is covered in my *Introducing Anthropology: An Integrated Approach*, fifth edition, and in a collection of contemporary articles edited by Aaron Podolefsky and Peter Brown, *Applying Anthropology: An Introductory Reader*, fifth edition.

I've written an extended version of the story of Henry Opukahaʻia, "The Homegoing," which appears in *Lessons from the Past: An Introductory Reader in Archaeology*, by Kenneth L. Feder. See also "The Life, Death, Archaeological Exhumation and Reinterment of Opukahaʻia (Henry Obookiah), 1792–1818," by Nicholas Bellantoni, Roger Thompson, David Cooke, Michael Park, and Cynthia Trayling in the Fall 2007 issue of *Connecticut History*.

For an update on the Hutterites, see "Solace at Surprise Creek" by William Albert Allard in the June 2006 *National Geographic*.

2
CHAPTER
The Evolution of Evolution

One touch of Darwin makes the whole world kin.
—George Bernard Shaw

Evolution and its application to the human species—how we descended from nonhuman ancestors, how we have changed over time into modern *Homo sapiens*, and how we are still changing—is a central theme of bioanthropology. As noted in Chapter 1, the *fact* of evolution is well supported by scientific examination—the idea has passed every scientific test applied to it. Scientists, however, are still debating the details of evolution and refining the *theory* that explains exactly how evolution operates. It took some time, though, for the scientific method to be applied to this idea.

How did our knowledge of the history of living organisms move from the realm of belief systems to the realm of science?

How did the scientific evidence for evolution develop?

"ON THE SHOULDERS OF GIANTS": EXPLAINING THE CHANGING EARTH

The Englishman Charles Darwin (1809–1882) is usually, and correctly, associated with our understanding of biological evolution (Figure 2.1). He is also popularly given credit for the very idea of evolution and for explaining and therefore proving it. This, however, is not entirely correct. Like any great scientific accomplishment, Darwin's was based on the work of many who came before him. He stood, as Isaac Newton said of himself, "on the shoulders of giants." Darwin's genius was in being able to take massive amounts of data and assorted existing ideas and, using an imagination possessed by few humans, put them all together into a logical, cohesive theory that made sense of the world and that could be examined by the methods of science.

The idea of **evolution** is simple enough: species of living things change over time, and under the right circumstances this change can produce new species of living organisms from existing ones. This idea was not new in Darwin's time. Anaximander, a Greek philosopher and astronomer of the sixth century BC, proposed that humans had arisen from other forms of life. He incorrectly thought we arose directly from fish, but rather than explaining his idea in supernatural terms, he used reasoning to explore the question of how animals survive in their environments, a question that would form the cornerstone of Darwin's idea (Harris 1981).

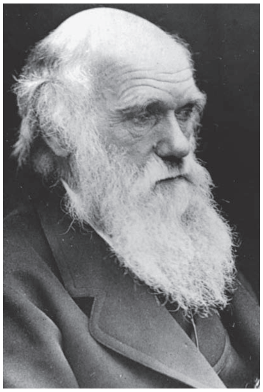


FIGURE 2.1
Portrait of Charles Darwin in 1869 by famed photographer Julia Margaret Cameron.

The Biblical Context

Many others over the next two thousand years also contemplated the origins of living things, but the modern story of evolutionary theory really began in seventeenth-century Europe, where the influence of the Bible was felt in all aspects of life, including science. Specifically, the ancient Judeo-Christian creation story—Adam and Eve, the Garden of Eden, the Flood and Noah's ark—was generally considered to be literally true. Thus, it was thought that the entire universe was created by supernatural processes over a period of six days and that, except for the matter of the great flood, the earth and its inhabitants were pretty much the same now as they were when created. One scholar, Irish archbishop James Ussher (1581–1656), used the assumption of biblical truth, as well as certain historical records, to help him calculate the date of the Creation and thus the age of the earth. In 1650 he reckoned that the Creation began at noon on Sunday, October 23, in the year 4004 BC. The earth was thus considered to be about 6,000 years old, and empirical facts about the earth were fitted into this biblical framework.

The Framework of "Natural Philosophy"

Dependence on the Bible for knowledge of the natural world was not to last. About the time Ussher was making his calculations, others were beginning to seek knowledge about the earth from the earth itself. What these "natural scientists," or "natural philosophers," saw forced them to reconsider what seemed to be the obvious lessons from the book of Genesis.

evolution Change through time; here, with reference to biological species.

The Evidence for Change Accumulates Another seventeenth-century scientist, Robert Hooke (1635–1703) recognized **fossils** of plants and animals—once thought to be mere quirks of nature—as the remains of creatures that had become extinct or that still existed but in different form. Living things, in other words, had changed.

Moreover, Hooke attributed these extinctions and changes to the fact that the earth itself had been continually undergoing change since the Creation. He even proposed a naturalistic explanation for Noah's flood; it was, he said, probably caused by earthquakes. So, since the earth is in a continual state of change, so are its inhabitants, changing as their environments are altered or becoming extinct if that alteration is too great.

Evidence for this idea of a changing earth came from the examination of the layers of rock and soil below the earth's present surface. These layers are the earth's **strata** (singular, *stratum*), and their study is called **stratigraphy** (Figure 2.2). One of the earliest scientists to discuss this was a Dane, Nicholas Steno (1638–1686). He suggested that the strata represented layers of sediments deposited by water in a *sequence*, the lower layers earlier and the higher layers later. The nature of the rock and soil of each stratum, and its fossil contents, showed the natural conditions at the time the stratum was deposited: what creatures existed, whether the area was under sea or on land, and so on. It became clear that neither the earth nor its inhabitants were stable and unchanging.

Catastrophism Was an Attempt to Reconcile the Evidence with a Biblical Time Frame Steno and Hooke, however, still believed in a biblical chronology. To Steno, the water-deposited layers of the stratigraphic sequences represented two events—the original water-covered earth on which God created land and plants and animals (Genesis 1) and the waters of Noah's flood (Genesis 6–8). The geological record, however, shows a vast amount of change, and the Bible provides only 6,000 years of the earth's history. So much change in such a short time, thought Steno and Hooke, required the presence of global catastrophic events such as earthquakes and volcanoes. Steno and Hooke and others who subscribed to this explanation are often referred to as **catastrophists.**

One well-known proponent of catastrophism was the French naturalist Georges Cuvier (1769–1832). He thought that a "prototype" of each creature had been created and that it and its environment had been planned to fit each other.

He also realized that life on earth had undergone major changes and believed that the entire plan of the Creation had been changed several times by the Creator and that the changes were manifested in a series of

fossils Remains of life-forms of the past.

strata Layers; here, the layers of rock and soil under the earth's surface.

stratigraphy The study of the earth's strata.

catastrophists Those who believe that the history of the earth is explained by a series of global catastrophes, either natural or divine in origin.

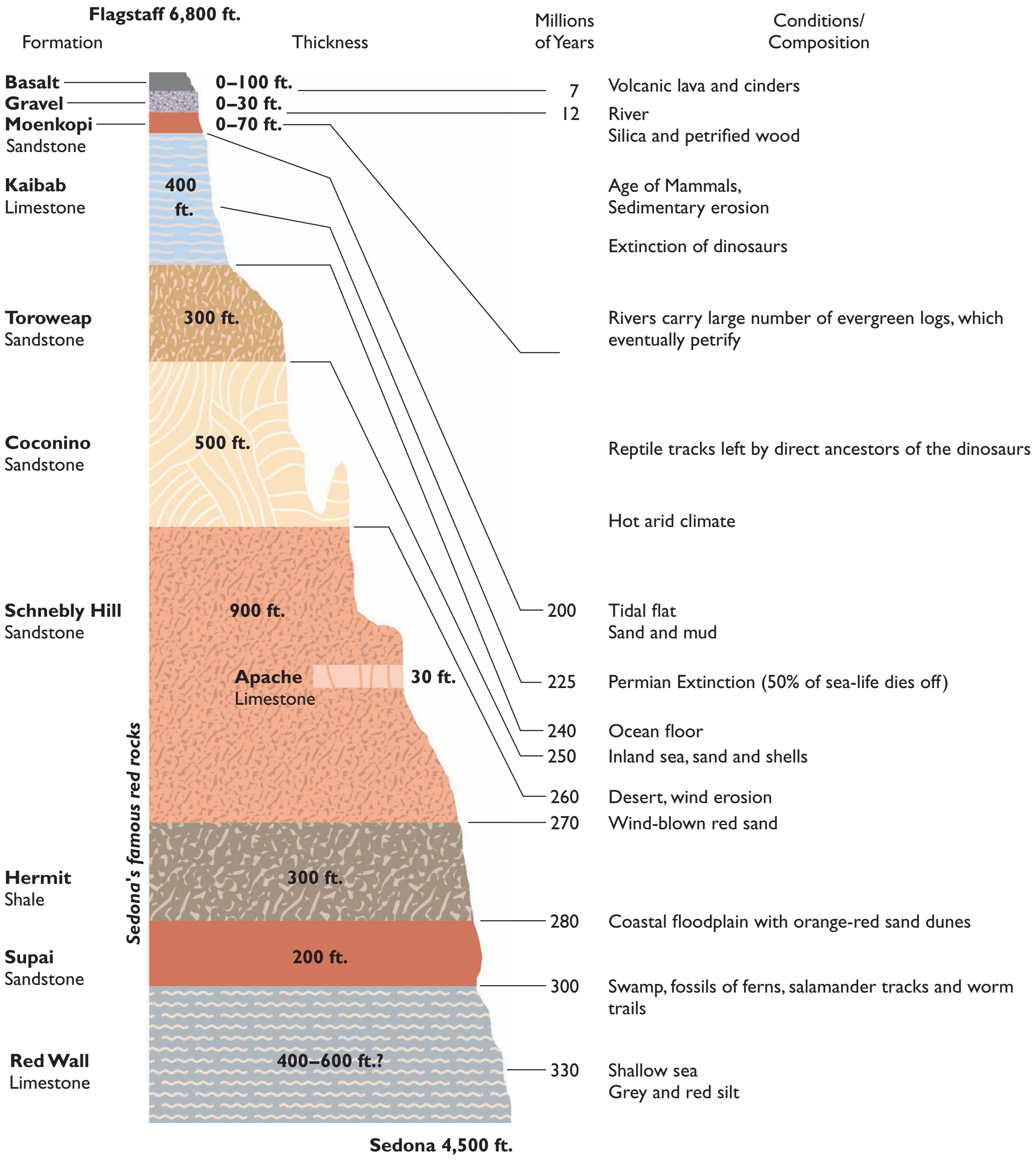

Flagstaff 6,800 ft.
Formation
Thickness
Millions of Years
Conditions/ Composition
Basalt
0–100 ft.
7
Volcanic lava and cinders
Gravel
0–30 ft.
12
River
Moenkopi Sandstone
0–70 ft.
Silica and petrified wood
Kaibab Limestone
400 ft.
Age of Mammals, Sedimentary erosion
Extinction of dinosaurs
Toroweap Sandstone
300 ft.
Rivers carry large number of evergreen logs, which eventually petrify
Coconino Sandstone
500 ft.
Reptile tracks left by direct ancestors of the dinosaurs
Hot arid climate
Schnebly Hill Sandstone
900 ft.
200
Tidal flat
Sand and mud
Apache Limestone
30 ft.
225
Permian Extinction (50% of sea-life dies off)
240
Ocean floor
250
Inland sea, sand and shells
260
Desert, wind erosion
270
Wind-blown red sand
Sedona's famous red rocks
Hermit Shale
300 ft.
280
Coastal floodplain with orange-red sand dunes
Supai Sandstone
200 ft.
300
Swamp, fossils of ferns, salamander tracks and worm trails
Red Wall Limestone
400–600 ft.?
330
Shallow sea
Grey and red silt
Sedona 4,500 ft.

FIGURE 2.2
This geological cross section of the area around Sedona and Flagstaff, Arizona, shows the variation in composition and thickness of the strata and some of the events represented in those strata.

global catastrophes that brought about the extinction of existing forms of life and prepared the way for newly created forms. In other words, he accepted that the world had changed but not that it had evolved, and not that new forms of life were modifications of older forms. Moreover, since humans were included only in the latest Creation, there was the implication that humans were somehow the Creator's highest, most perfect form of living thing.

Uniformitarianism Ushers in the Modern Approach Catastrophism enjoyed a degree of popularity because it seemed to reconcile natural evidence with a biblical time frame. But strict catastrophism did not stand up to further scientific observation and examination. The French scholar Comte Georges-Louis Leclerc de Buffon (1707–1788) concluded that although catastrophic events do occur, they are rare and so "have no place in the ordinary course of nature." Instead, the earth's history is mainly explained by "operations *uniformly* repeated, motions which succeed one another without interruption" (emphasis mine). Thus, much of the earth's geological history could be explained by normal, everyday, uniform processes—the things taking place before our eyes, such as erosion and deposition of sediments in water. This idea is called **uniformitarianism.** For such processes to account for all the changes recorded in the earth's strata, however, the earth would have to be older than 6,000 years. Buffon was among the first to propose a longer history for the planet.

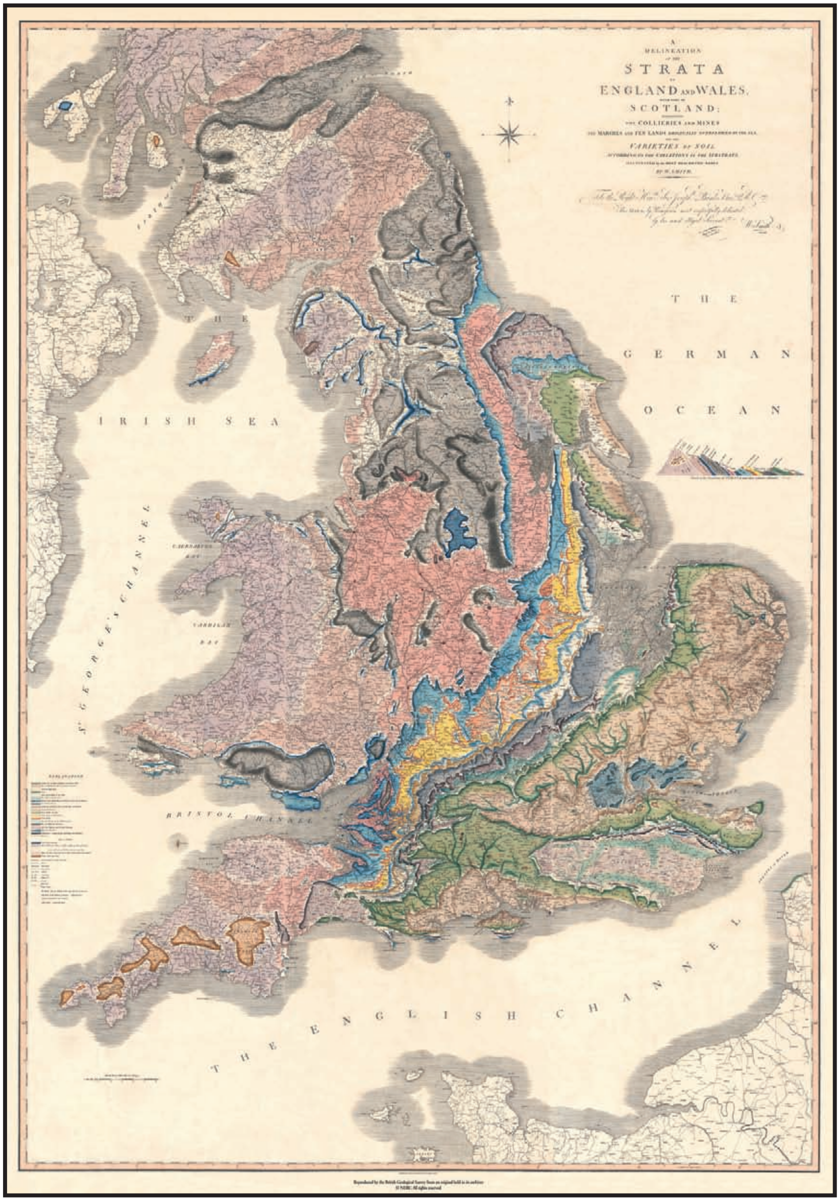
A Scotsman, James Hutton (1726–1797), elaborated on the idea. Hutton saw the processes of deposition and erosion as part of a self-regulating system and he suggested that the earth was much older than 6,000 years, indeed having "no vestige of a beginning—no prospect of an end."

The English surveyor and geologist William Smith (1769–1839) formalized the description of the evidence for change in the earth—the strata and their fossil content. Smith, whose work earned him the nickname "Strata," documented the patterns of strata and fossils across England, Wales, and Scotland and produced the first geological map of any area of the world (Figure 2.3).

Charles Lyell (1797–1875), born in Scotland the year Hutton died, expressed an extreme version of uniformitarianism. He believed that the earth itself was fairly uniform across time, that the earth has been, and always will be, basically the same. Changes certainly occur, but they occur, said Lyell, just in the details, not in the overall appearance of the earth or in its life-forms. Moreover, these changes occur in great cycles. He thought, for example, that dinosaurs, though extinct at the moment, would eventually reappear.

uniformitarianism The idea that present-day geological processes can also explain the history of the earth.

FIGURE 2.3
William Smith's 1815 map, titled "A Delineation of the Strata of England and Wales, with Part of Scotland . . ." The original, more than 6 by 8 feet, is at the Geological Society of London.


A DELINEATION OF THE STRATA OF ENGLAND AND WALES, WITH PART OF SCOTLAND;
VARIETIES OF SOIL
BY W. SMITH.
THE GERMAN OCEAN
IRISH SEA
ST. GEORGE'S CHANNEL
BRISTOL CHANNEL
THE ENGLISH CHANNEL

Today we understand that Lyell's idea about the earth changing only in its details and in great cycles is incorrect. The earth's history is a complex chain of events leading to other events, a continual sequence of changes—major and minor—never to be repeated. The dinosaurs are extinct; they will never return (Figure 2.4).

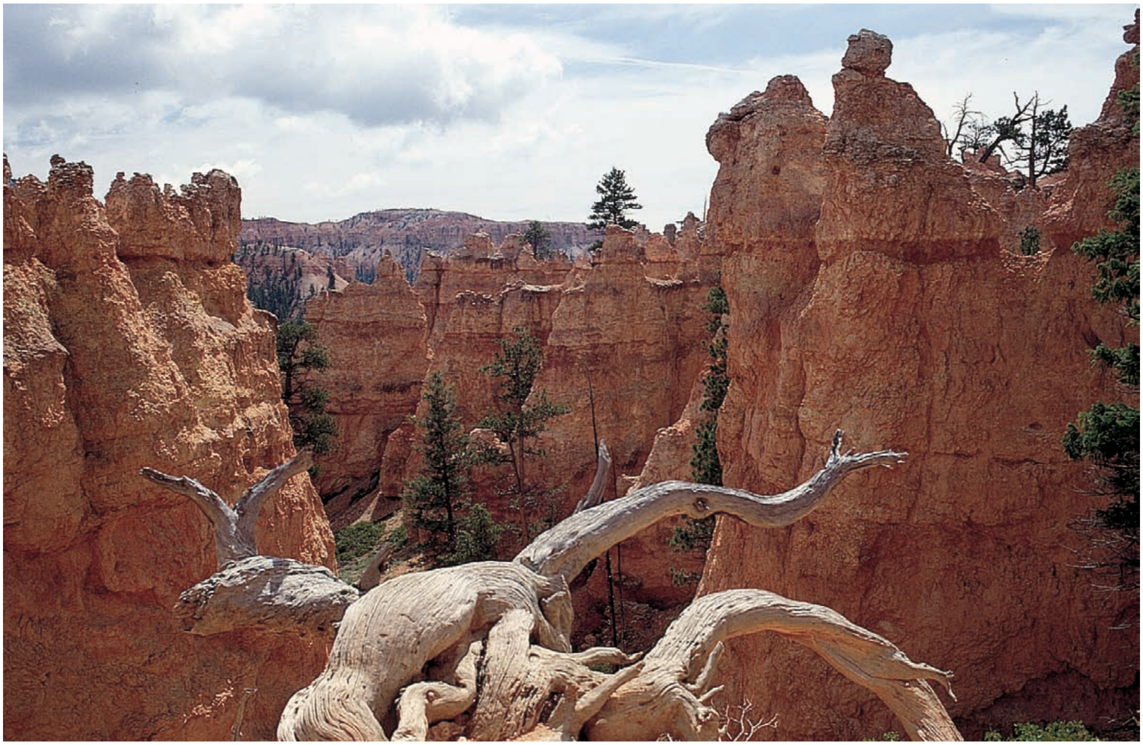


FIGURE 2.4
Utah's Bryce Canyon shows the results of a long series of geological processes, especially the laying down of strata and subsequent erosion, over millions of years.

Despite what turned out to be some incorrect notions, however, Lyell's influence was great. Not only did he expand on the work of Hutton and others, he also began the explicit examination of geological data, bringing it fully into the realm of natural science. For example, he attempted to estimate the age of the Mississippi Delta (Figure 2.5).

Through the work of Hooke, Steno, Hutton, Smith, and Lyell—and many others—the study of the earth shifted from the supernatural to the natural. Scientists sought data about earth's history from the earth itself, not from the presuppositions of belief systems. As a result, by the early nineteenth century, our world was viewed through the interacting perspectives of constant change brought about by observable processes over vast amounts of time.

Lyell put these ideas down in his three-volume *Principles of Geology*, first published between 1830 and 1833. Among those weighing Lyell's ideas was a young British naturalist, Charles Darwin, who took the first volume of Lyell's book with him as he embarked, in 1831, on a round-the-world voyage of scientific exploration.

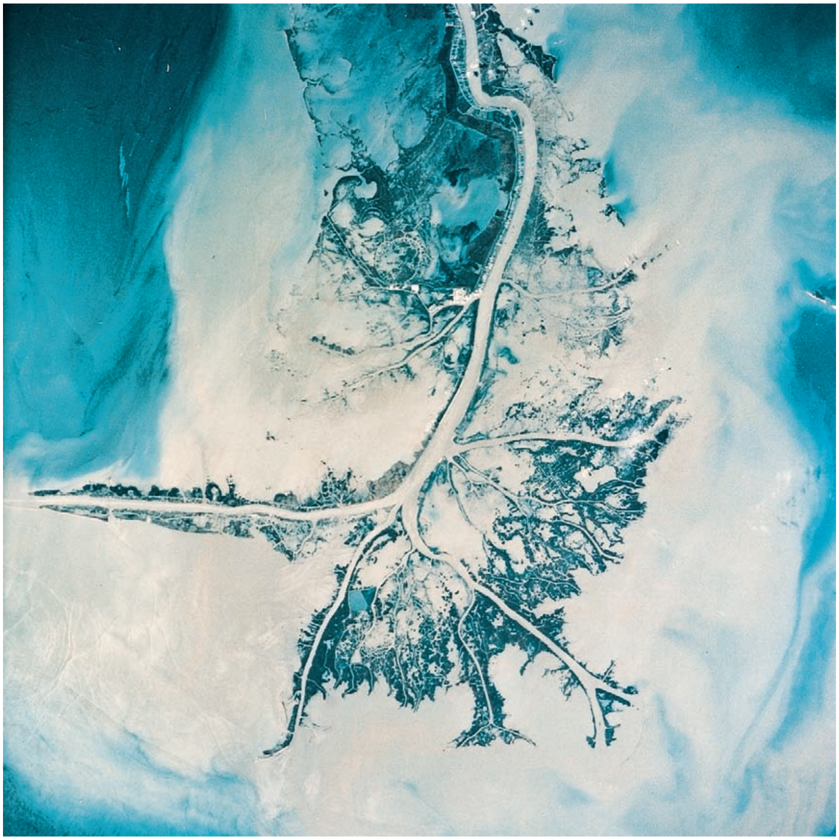


FIGURE 2.5
Aerial view of the Mississippi Delta. By estimating the amount of material deposited in the delta (the delta-shaped [Δ] deposit of sand and soil at the mouth of a river), Charles Lyell concluded (although incorrectly) that it was 100,000 years old.

"COMMON SENSE AT ITS BEST": EXPLAINING BIOLOGICAL CHANGE

Darwin's Predecessors

The view of life on earth as static and unchanging is exemplified by the work of Carl von Linné (1707–1778), better known to us as Carolus Linnaeus, whom we will discuss in detail in Chapter 7. Linnaeus, who devised the system of scientific names we still use to classify living things, initially thought that all species of plants and animals had been divinely created in their present forms and numbers. But Linnaeus, a keen observer of nature, came to recognize (as had Hooke before him) that some sort of change had taken place—that fossils, for example, represented species that had become extinct and that new species could arise.

Gradually, then, through the observations and interpretations of all the scientists discussed so far, it became clear that life on earth had undergone change, just as had the earth itself, and that this change required scientific explanation using a uniformitarian approach. But this idea—then referred to as the *transmutation of species*—was a more controversial matter than the idea of a changing earth. For if other forms of life had arisen and changed over eons of time by uniform natural processes, then it followed that the same should apply to humans. So, even after it became obvious that life had "evolved" (as we now phrase it), just *how* this had taken place mattered a great deal.

There were many who addressed this issue from a uniformitarian position, including Charles Darwin's grandfather, Erasmus Darwin (1731–1802), but one of the most influential was the French naturalist Jean-Baptiste de Lamarck (1744–1829). Lamarck emphasized Hooke's conclusion that plants and animals are **adapted** to their environments; that is, each kind of living organism has physical traits and behaviors that allow it to survive under a given set of natural circumstances. When environments change—as the stratigraphic record shows they do—organisms must change if they are to continue to exist.

Lamarck was quite correct that organisms undergo change and that this change is connected to the environment. He erred, however, in his explanation of how this change occurs and in his idea that change is **progressive,** going from imperfect to perfect by a process of increasing complexity. It should be obvious which species Lamarck thought was the most perfect and complex. This was the appeal of the idea of progressive evolution: if life itself changed through time, at least *we* were what it was changing toward.

Lamarck's mechanism for this progressive change is called the **inheritance of acquired characteristics,** an old idea that Lamarck formalized in his 1809 *Philosophie zoologique*. He wrote:

> When the *will* guides an animal to any action, the organs which have to carry out that action are *immediately stimulated* to it by the influx of *subtle fluids*. . . . Hence it follows that numerous repetitions of these organised activities strengthen, stretch, develop and *even create* the organs necessary to them. . . . Now every change that is wrought in an organ through habit of frequently using it, is subsequently *preserved by reproduction*. . . . Such a change is thus handed on to *all succeeding individuals* in the same environment, without their having to acquire it in the same way that it was actually created. (Harris 1981:116–17; emphases mine)

adaptation The state in which an organism is adjusted to and can survive in its environment through its physical traits and behaviors. Also, the process by which an organism develops this state through natural processes.

progressive In evolution, the now-discounted idea that all change is toward increasing complexity.

inheritance of acquired characteristics The incorrect idea that adaptive traits acquired during an organism's lifetime can be passed on to its offspring.

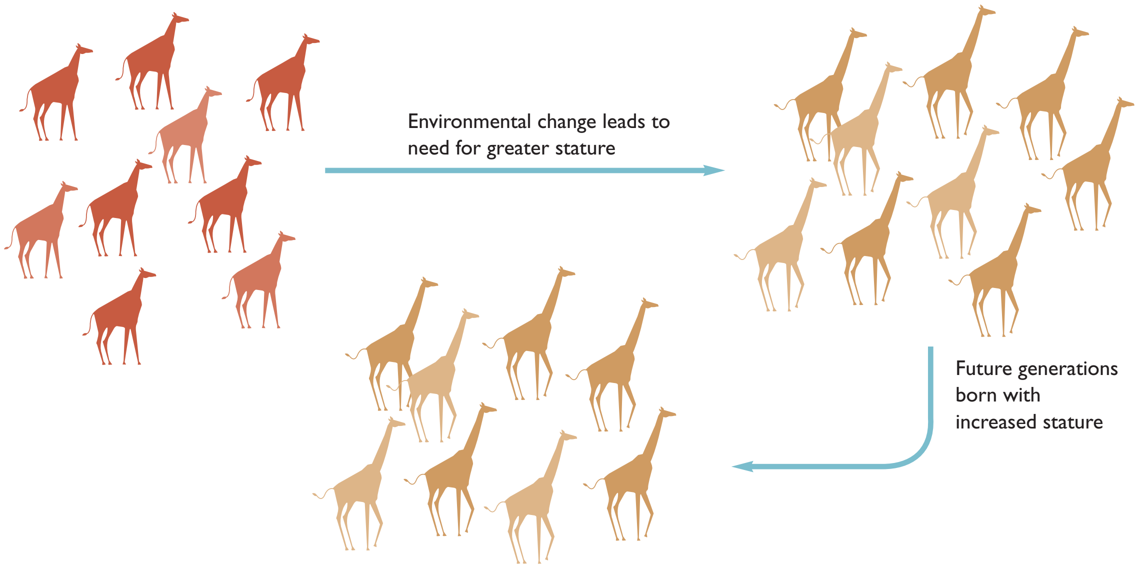

Environmental change leads to need for greater stature
Future generations born with increased stature

FIGURE 2.6
Lamarck's model of inheritance of acquired characteristics applied to the evolution of long necks and tall bodies in giraffes. In the past, giraffes were short, but environmental change altered their food source, placing the foliage they ate high up in the trees. Confronted with this problem, *each giraffe* was able to stretch its neck and legs enough to reach the leaves. This greater height was automatically passed on to the giraffes' offspring, which had to make themselves even taller, and so on, giving rise to the 18-foot-tall giraffes of today.

As a famous (and probably overused) example, Lamarck explained the long necks and legs of giraffes in the following way: In the past, giraffes were short, but some environmental change altered their food source, placing the foliage they ate high up in the trees. Confronted with this problem, each giraffe was able to stretch itself enough to reach the leaves. This greater height was automatically passed on to the giraffes' offspring, which had to make themselves even taller. And so on (Figure 2.6).

One reason that Lamarck's idea was popular was that it was one of the first detailed, lengthy, scientific treatments of evolution. Lamarck even spelled out how he used the scientific method by specifying the data that would be required to falsify his model. It was a comfortable explanation for an uncomfortable topic. At least, according to Lamarck's hypothesis, life changed in a particular (and very human-oriented) direction, and it changed by a process that was unfailing and dependent on something inherent to the organism—Lamarck called it "will." It even followed that no organisms ever become extinct. Creatures represented only by fossils were simply creatures that had undergone so much change they now looked very different.

But observation and logic produced some major objections to Lamarck's concept. Traits acquired during an organism's lifetime cannot be inherited by its offspring. A bodybuilder's children will not automatically be born with bulging muscles. Further, it was hard to see how an organism's "will" could change its color or produce a new organ or make a giraffe taller. And just what is the "subtle fluid" that is supposed to bring all this about?

Charles Darwin

Charles Darwin was born (in 1809, the same year Lamarck's book was published) into a world that accepted the *fact* of biological change but was still in search of a *mechanism* for that change. It was Darwin who would provide the mechanism that has withstood over a century and a half of scientific examination.

The story of Darwin's life and scientific work is a fascinating one (see the list of biographies in this chapter's "Suggested Readings"). For the purpose of our story, however, we can simply say that Darwin recognized an important fact not fully appreciated by many of his predecessors or contemporaries. In his work in his native England and especially on his famous voyage around the world on the HMS *Beagle* (1831–1836; Figure 2.7), Darwin realized the incredible degree of variation that exists within each living species (Figure 2.8). If Lamarck were correct, one would expect every member of a particular species to look pretty much

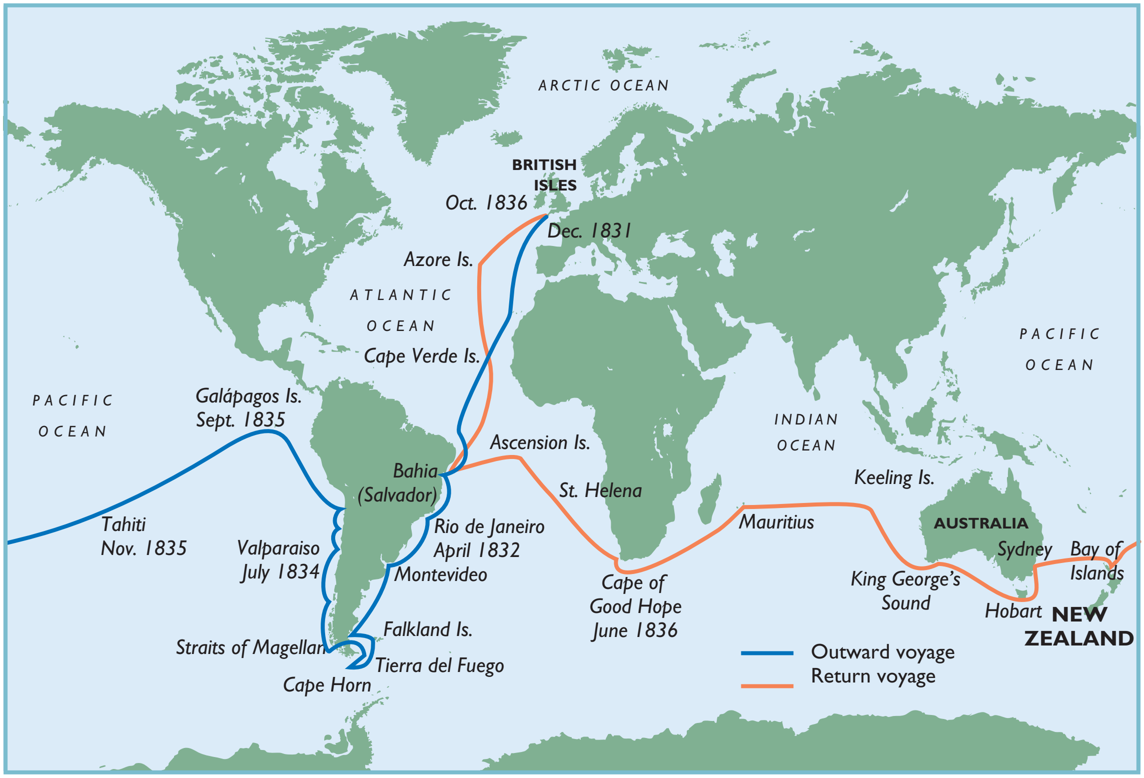

ARCTIC OCEAN
BRITISH ISLES
Oct. 1836
Dec. 1831
Azore Is.
ATLANTIC OCEAN
Cape Verde Is.
PACIFIC OCEAN
PACIFIC OCEAN
Galápagos Is. Sept. 1835
Ascension Is.
INDIAN OCEAN
Bahia (Salvador)
St. Helena
Keeling Is.
Tahiti Nov. 1835
Valparaiso July 1834
Rio de Janeiro April 1832
Montevideo
Mauritius
AUSTRALIA
Sydney
Bay of Islands
Cape of Good Hope June 1836
King George's Sound
Hobart
NEW ZEALAND
Falkland Is.
Straits of Magellan
Tierra del Fuego
Cape Horn
Outward voyage
Return voyage

FIGURE 2.7
Route of Darwin's voyage aboard the HMS *Beagle* from 1831 to 1836. This trip provided Darwin with observations and thoughts vital to his formulation of the theory of natural selection. Especially famous and important was his visit to the Galápagos Islands in the eastern Pacific.

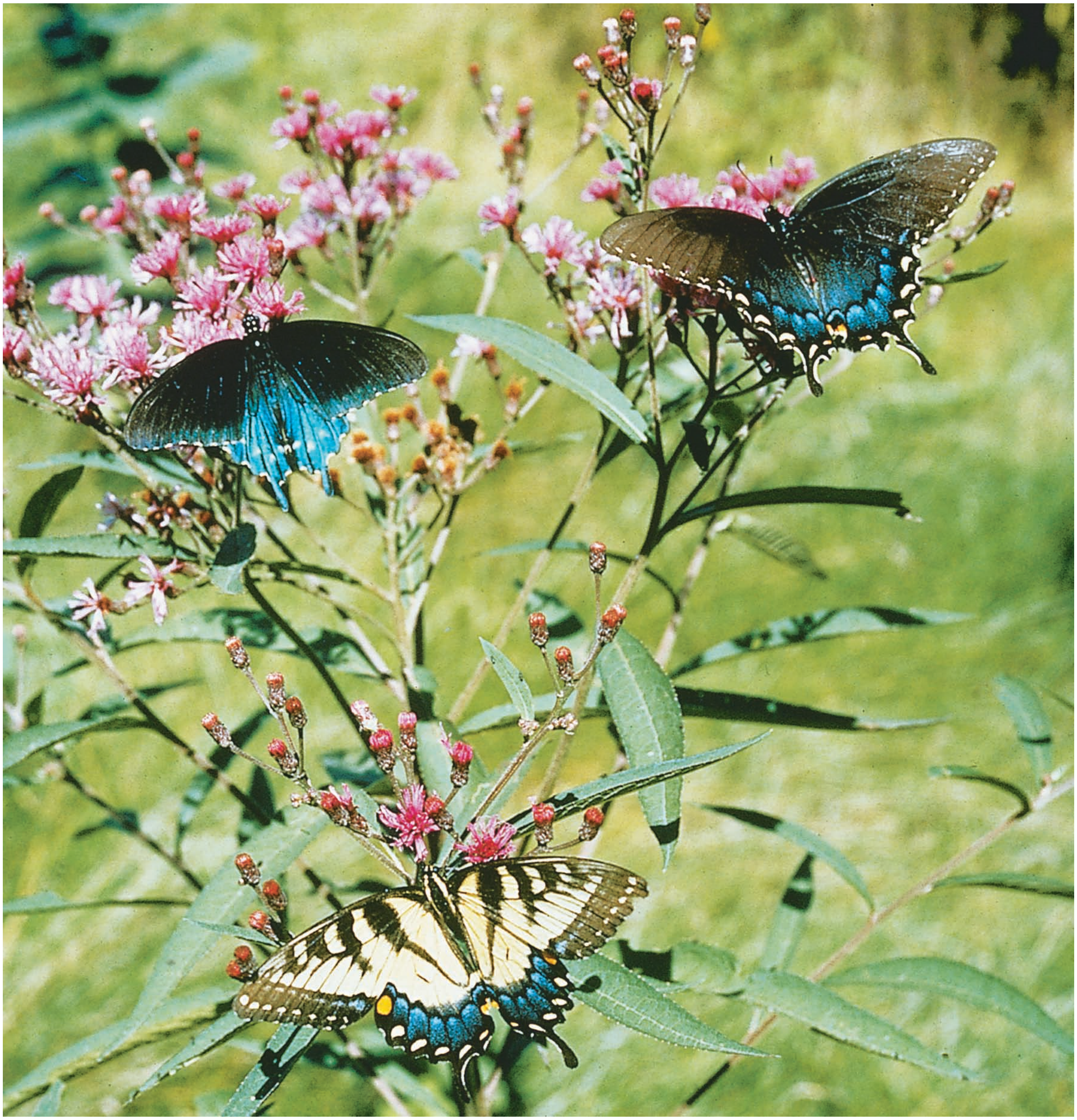


FIGURE 2.8
Variation within a population represents the raw material for natural selection. The tiger swallowtail butterflies (*upper right and bottom*) are members of the same species. The dark tiger swallowtail is a mimic of the pipe-vine butterfly (*left*), which is protected from predation by its foul taste.

the same because they all would have responded identically to the same environmental circumstances. Darwin saw that this was clearly not the case. Variation always exists, no matter how well adapted a species might be. What tipped Darwin off to this fact of nature were his observations of domestic species such as pigeons, carefully bred for certain features but still showing physical variation every generation. In each generation, breeders would have to choose for mating only those individuals possessing the features they desired. The goal was to eliminate undesirable traits and accumulate desirable ones.

Darwin also took a clue from the work of English economist Thomas Malthus (1766–1834). Malthus argued that human populations, if unchecked, increase at a more rapid rate than do resources. Thus, there is competition within any population over those resources, and this is what keeps populations in check.

Darwin reasoned that the same things happened in nature. Some of the natural variation within a species would make a difference in the success, or **fitness,** of individuals. The better-adapted individuals would tend to be more reproductively successful. Their traits would be passed on to more offspring than would those of the less well adapted. Over time, then, some traits would accumulate while others would decrease in frequency or even be eliminated. If the environment to which a species is adapted changes, it stands to reason that the fitness value of certain traits might also change, so the process described might proceed in a different adaptive direction—what was once adapted might now be neutral or perhaps even poorly adapted.

So, while Lamarck thought that variation *arose when it was needed,* Darwin understood that variation *already existed.* Because Darwin lived before the processes of genetics were understood, he did not know where this variation came from, but his observations showed it was a fact; and he realized that nature, like a plant or animal breeder, "selects" better-adapted individuals for more successful reproduction. Darwin called this process **natural selection.**

Thus, according to Darwin's model, giraffes didn't become steadily taller and taller in response to one environmental change. Rather, over many millennia, various environmental factors selected for certain expressions of many traits, resulting today in these tallest of living mammals.

Several important ideas follow from natural selection:

1. It becomes clear that evolution by natural selection has no particular direction. Organisms do not "progress" to increasingly complex

fitness The relative adaptiveness of an individual organism, measured ultimately by reproductive success.

natural selection Evolutionary change based on the differential reproductive success of individuals within a species.

forms, as Lamarck thought, but evolve to simply stay adapted to their environments or, if possible, become readapted to changed environments. Variation is not "willed." It results from random processes that we now understand from the study of genetics (see Chapter 3).

2. It is also clear that such a process, using random rather than directed or "willed" variation, is not foolproof. Species do become extinct, usually when the environment changes so extensively or rapidly that none of the existing variation within a species is adaptive. Extinction is, in fact, the norm. Nine-tenths of all species that have ever lived are now extinct.
3. It follows that *new* species can arise from this basic process. If populations within a species become environmentally separated, these populations will exist under different selective pressures—different traits will be differently adapted to each environment. Over time, then, a single species may give rise to one or more new species. This, in fact, was what Darwin was ultimately trying to explain, as indicated by the title of his most famous work, *On the Origin of Species by Means of Natural Selection,* first published in 1859. (See Chapter 5.)

Darwin's idea generated some controversy, which was perhaps why he delayed publishing his book. We know he understood natural selection sometime in the late 1830s, yet it was not until more than twenty years later that he made it public. Even then, he did so only because a younger, less well-known naturalist, Alfred Russel Wallace (1823–1913), independently came up with the same idea, and Darwin was urged by friends to rush his conclusion into print.

To Darwin's surprise, by the time his book sold out on its first day of publication, the scientific community and much of the informed public were ready to accept the idea, even with its implications. Natural selection—the mechanism of evolution—was hailed as a major scientific breakthrough and remains today a classic example of scientific reasoning, what Darwin's friend Thomas Henry Huxley called "common sense at its best."

The Modern Theory of Evolution

At about the time Darwin was writing *Origin of Species,* a monk in what is now the Czech Republic was answering Darwin's question about the source of variation. After years of undocumented research on several species of

Contemporary Reflections

Has Science Dehumanized Society?

To many, the story recounted in this chapter is one of science *versus* belief systems, specifically religious belief. A popular assessment of Darwin's contribution is that by "proving" evolution he "disproved" the Bible. As we will see in Chapter 5, there is still a substantial contingent today that feels that the very idea of evolution is antireligious.

And it's not just the science of evolution. From Mary Shelley's *Frankenstein* (1818) to modern blockbuster movies such as the *Jurassic Park* series, science in general is seen as a potential evil, something that is far too easily abused and that, when abused, wreaks havoc on people and their societies. People often use the phrase "playing God" when referring to scientific endeavors that they perceive as affronts to human spirit and individuality. Science is blamed for many of today's social and environmental ills—and there *are* plenty of them—from global climate change to radioactive contamination to the proliferation of weapons of mass destruction.

There are three errors in this view of science. First, although science has put forth and scientists have embraced ideas that have resulted in human suffering, one of the hallmarks of science is its ability for self-correction. The eugenics movement, for example—which held that many human behaviors were hereditary and that therefore selective breeding could improve our species—resulted (even in the United States) in the forced sterilization of many individuals who were deemed less fit because of some characteristic that society felt undesirable (below-average intelligence, for instance, or having borne illegitimate children). This practice is abhorrent, but through scientific progress we now know much more about the nature of human heredity, and such mistakes are at least unlikely in the future.

Second, this view of science ignores the fact that *anything* may be a danger if used incorrectly or for nefarious purposes. One has but to examine world history to see that religious ideals are not always put to positive use. Indeed, many of today's bloody hostilities are the result of religious conflict—often involving religions that specifically prohibit the taking of human life.

Third, in focusing on the negative results of science, we all too easily forget about the positive results. Today's most vocal critics of science still promote their ideas on television and over the Internet; they travel in airplanes and enjoy all the medical and nutritional benefits of a modern scientific society. The astronomer Carl Sagan (1934–1996) once asked a group of people how many of them would not be alive today if it weren't for modern medical technology. Most raised their hands. (I tried this with a class of undergraduates, average age about 20, and still about half raised their hands.)

But didn't Darwin set the stage for this seeming conflict by disproving the Bible with his theory of evolution? Not at all. He *did* show that one literal interpretation of one part of one book of the Bible failed to account for observations of biology in the real world. In no way, however, did his idea of evolution refute a whole religious worldview, nor need it conflict with one's personal sense of the spiritual.

It is not knowledge or ideas, scientific or otherwise, that are dangerous; it is *how* they are used that matters. Ignorance, however, is dangerous, and it is ignorance that dehumanizes us.

plants and animals, Gregor Mendel (1822–1884) derived the basic laws of genetics by experimenting with pea plants in the garden of his monastery. These laws (which we'll cover in the next chapter) not only explained one source of biological variation but also showed why and how offspring tend to resemble their parents. Basic laws of genetics and biological variation are crucial to natural selection and the origin of new species.

Mendel died in relative obscurity (Darwin never learned of his work), and his writings languished in libraries until 1900, when they were rediscovered independently by three European scientists who realized that Mendel's work carried implications far beyond some interesting facts about pea plants. They understood that genetics filled in those pieces that Darwin acknowledged were missing from his process.

During the twentieth century, the history of evolutionary theory became more complex, with many more scientists refining and adding to the theory especially, at first, showing how Mendelian genetics, biological diversity, and natural selection interact in evolution.

But all the work of the past hundred years has been built on the thoughts and discoveries of Darwin, Lyell, Hooke, and many others. All the men and women whose investigations have led to our modern theory of evolution (which we will cover in the next three chapters) would freely agree that they have stood on the shoulders of these giants (Table 2.1).

NOTE: Since the topic of this book is the human species, it may have struck you that one-half of our species—namely, women—is distinctly missing from the preceding historical discussion. This has nothing to do with differences in intellect and everything to do with the social, educational, and occupational limits placed on women until fairly recently. (Remember, women have been able to vote in the United States for less than 100 years.) Simply put, no women played major roles during most of the history of evolutionary theory. This is largely true for science in general. Women who were involved in the sciences early on were often amateurs, such as Mary Anning (1799–1847), an English naturalist and fossil hunter, and Beatrix Potter (1866–1943), a fungi expert better known as the creator of Peter Rabbit and other beloved characters of children's literature. Women scientists of the past were also considered anomalies and sometimes linked to men, such as the Polish chemist Marie Skłodowska-Curie (1867–1934), often mentioned along with her husband, Pierre (1859–1906).

In the twentieth century, women became more prominent in the sciences. A few notable examples from the biological sciences are Barbara McClintock (1902–1992), who won a Nobel Prize for her work in genetics; Rosalind Franklin (1920–1958), who probably *should* have shared a Nobel with James Watson and Francis Crick for discovering the structure of DNA; and Dian Fossey (1932–1985), Jane Goodall (b. 1934), and many other women involved in primate studies and other aspects of biological anthropology (whom we shall meet later on).

TABLE 2.1
Early Figures in Evolutionary Theory (before 1900)

	Approx. Date of Publication	*Contribution*
James Ussher (1581–1656)	1650	Calculation of the age of earth, using biblical data
Robert Hooke (1635–1703)	1660s–90s	Fossils as evidence of change Importance of environmental change
Nicholas Steno (1638–1686)	1669	Stratigraphy
Carolus Linnaeus (1707–1778)	1758	System of scientific names Recognition of extinction and possibility of new species
Comte Georges-Louis Leclerc de Buffon (1707–1788)	1749	Uniformitarianism Longer time frame for age of earth
James Hutton (1726–1797)	1795	Uniformitarianism Natural cycles Longer time frame for age of earth
Jean-Baptiste de Lamarck (1744–1829)	1809	Adaptation Inheritance of acquired characteristics Progressive evolution
Thomas Malthus (1766–1834)	1789	Relationship between population and resources
William Smith (1769–1839)	1815	First geological map showing strata
Georges Cuvier (1769–1832)	late 1700s, early 1800s	Ideal prototypes Climatic alterations Extinction Catastrophism
Charles Lyell (1797–1875)	1830–33	Uniformitarianism Scientific investigation
Charles Darwin (1809–1882)	1859	Natural selection Origin of species
Gregor Mendel (1822–1884)	1860s	Laws of inheritance
Alfred Russel Wallace (1823–1913)	1859	Natural selection

SUMMARY

The Judeo-Christian belief system, as set down in and interpreted from the Bible, was long seen as both a belief system and a source of literal knowledge. As scholars began looking more objectively at nature itself, however, their observations and the rational conclusions they drew from them showed clearly that knowledge of the heavens, the earth, and the earth's inhabitants required the methods of science. As the scientific method was applied to the study of the earth, scientists gradually learned to give up their presuppositions.

Charles Darwin, adhering faithfully to the spirit of scientific methodology, was able to synthesize his observations and thoughts with those of many others and to formulate a theory that made possible the work that has led to our modern knowledge of the nature and evolution of living things.

QUESTIONS FOR FURTHER THOUGHT

1. The scientific research and ideas of many early biologists and geologists were influenced by philosophical concepts. Do you think such influences ended with people like Darwin? Can you think of a modern scientific matter that may be influenced by beliefs?
2. Whereas biological evolution is not Lamarckian, the evolution of culture is. How so?
3. There are those who say that certain areas of scientific research should be avoided either because their results might be misused or because the facts generated might be unpleasant. What sorts of research do you think these people might be referring to? How would you respond to such cautions?

KEY TERMS

evolution
fossils
strata
stratigraphy
catastrophists
uniformitarianism
adaptation
progressive
inheritance of acquired characteristics
fitness
natural selection

SUGGESTED READINGS

The history of the study of evolution is covered in *Readings in the History of Evolutionary Theory* by Ronald K. Wetherington, which contains numerous sections from original works, and in John C. Greene's old but classic *The Death of Adam*. The impact of Darwin's work on modern knowledge in general is the theme of Philip Appleman's *Darwin: A Norton Critical Edition*, second edition.

There are a number of good biographies of Darwin. I especially like *Charles Darwin: A New Life*, by John Bowlby, and *Charles Darwin: Voyaging* and *Charles Darwin: The Power of Place*, by Janet Browne.

For online access to Darwin's writings, see http://darwin-online.org.uk and www.darwinproject.ac.uk.

See the November 2005 issue of *Natural History*, nearly all of which is devoted to Darwin and evolutionary theory, and "Darwin's Big Idea," by David Quammen, in the November 2004 issue of *National Geographic*. See also "Darwin's Enduring Legacy," by Kevin Padian, in the 7 February 2008 *Nature*.

For more on the fascinating life and work of Alfred Russel Wallace, see *Bright Paradise: Victorian Scientific Travelers*, by Peter Raby; *In Darwin's Shadow: The Life and Science of Alfred Russel Wallace*, by Michael Shermer; and "Missing Link," by Jonathan Rosen in the 12 February 2007 *New Yorker*.

William "Strata" Smith's eventful life is chronicled in Simon Winchester's *The Map That Changed the World: William Smith and the Birth of Modern Geology*.

Paleontologist and science historian Stephen Jay Gould wrote many wonderful essays about the history of evolution and other scientific topics and the personalities involved. These can be found throughout his books *Ever Since Darwin*, *The Panda's Thumb*, *Hen's Teeth and Horse's Toes*, *The Flamingo's Smile*, *Bully for Brontosaurus*, *Eight Little Piggies*, *Dinosaur in a Haystack*, *Leonardo's Mountain of Clams and the Diet of Worms*, *The Lying Stones of Marrakech*, and *I Have Landed*. I highly recommend all of these.

3

CHAPTER

Evolutionary Genetics

The laws governing inheritance are for the most part unknown.
—Charles Darwin

Important features of Darwin's natural selection were two seemingly contradictory facts: (1) offspring tend to resemble their parents, but (2) there is a continual production of biological variation among members of a species and from generation to generation. Both facts were obvious enough to careful observers such as Darwin. But, as Darwin freely admitted, science was largely ignorant of the source of those facts, in other words, of how inheritance worked. A popular idea of Darwin's time assumed that inheritance was "blending"—a mixture of material from both parents.

Observations of nonblending traits such as sex may have led Gregor Mendel to begin experiments to determine just how inheritance operates. The laws he derived are still recognized today as the basis of genetics, although, of course, they have been added to greatly. The most basic and perhaps most important of Mendel's contributions was his conclusion that inheritance does not involve the blending of substances but, rather, is **particulate.** He showed that traits are passed on by individual particles according to very specific principles. Mendel called these particles "factors"; we call them **genes.** We'll now survey the aspects of modern genetics pertinent to bioanthropology by addressing the following questions:

What are genes, and how do they produce the traits that make a pea plant or a human being?

What do we know about the nature of the human genome?

What are the basic laws of inheritance?

What processes bring about the variation we see among members of a species and between parents and offspring?

HOW GENES WORK

We begin with something Mendel could not possibly have understood: how the genetic code operates at the chemical level. We now understand that the genetic code is a set of instructions for the production (or synthesis) of **proteins** from **amino acids.** Proteins are the basic building blocks of an organism's cells, shaping the cells, supporting the cells' internal structures, linking cells, and building membranes, muscles, and connective tissue. In a form called **enzymes,** proteins are responsible for the cells' chemical reactions. All organisms are composed of cells (Figure 3.1), so it can logically be said that all living things are based on proteins. Even the nonprotein substances found within a living organism—such as the calcium in your bones—are regulated by proteins.

The genetic code is found in the nucleus of cells, on long strands called **chromosomes** (see Figure 3.7). One component of these—**deoxyribonucleic acid (DNA)**—carries the code. DNA is like a ladder with its ends twisted in opposite directions (Figure 3.2). This shape is referred to as a *double helix*. The sides of the ladder provide structural stability. The rungs of the ladder are the code. They are made up of pairs of bases (a family of chemicals) bonded in the middle. Only four bases are involved: adenine (A), thymine (T), cytosine (C), and guanine (G), and they are only paired in A-T or T-A and C-G or G-C combinations. Thus, if we know the sequence of bases on one side of the DNA helix, we can correctly predict the sequence on the other side.

The first function of this pairing is to enable the DNA molecule to make copies of itself during cell division. During cell division the helix unwinds, and each strand, with its now unpaired bases, picks up the proper complementary bases, which are in solution in the cell. This is called **replication.** Thus, when the whole cell divides, each new *daughter cell* has a complete set of DNA base pairs (Figure 3.3). This is the process of **mitosis.**

Each base (A, T, C, G) is like a letter in an alphabet. We refer to each consecutive sequence of three DNA bases as a **codon.** Codons are like words made up of exactly three letters. Each genetic word stands for a particular amino acid (with a few words meaning "stop," the equivalent of a period at the end of a sentence). A string of codons —or chain of amino acids—is a protein:

FEATURE	ANALOGUE	MEANING
base (A, T, C, G)	letter	
codon	word	amino acid
gene	sentence	protein

particulate The idea that biological traits are controlled by individual factors rather than by a single all-encompassing hereditary agent.

genes Those portions of the DNA molecule that code for a functional product, usually a protein.

proteins Molecules that make cells and carry out cellular functions.

amino acids The chief components of proteins.

enzymes Proteins that control chemical processes.

chromosomes Strands of DNA in the nucleus of a cell.

deoxyribonucleic acid (DNA) The molecule that carries the genetic code.

replication The copying of the genetic code during cell division.

mitosis The process of cell division that results in two exact copies of the original cell.

codon The three-base sequence that codes for a specific amino acid. Technically, the sequence on the mRNA.

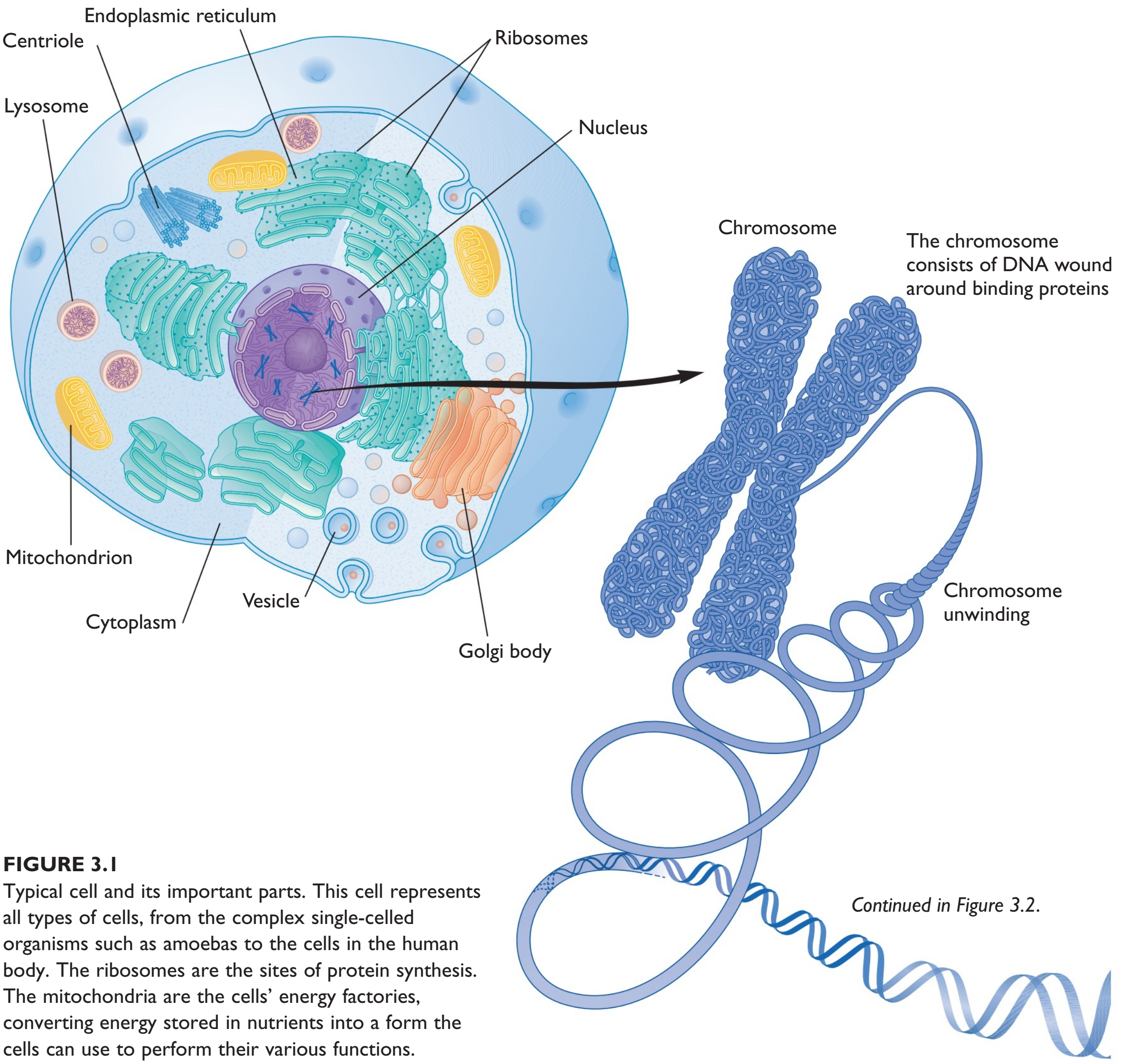

Endoplasmic reticulum
Centriole
Lysosome
Ribosomes
Nucleus
Mitochondrion
Cytoplasm
Vesicle
Golgi body
Chromosome
The chromosome consists of DNA wound around binding proteins
Chromosome unwinding

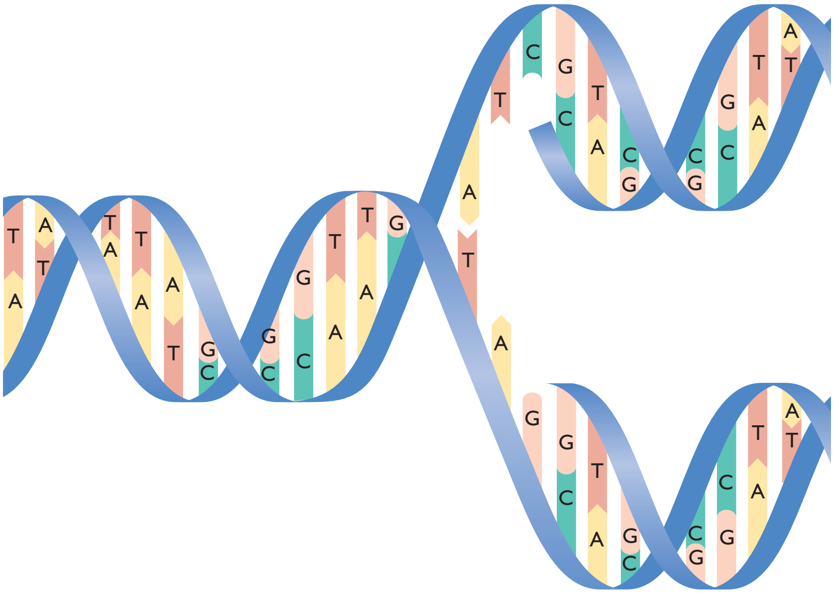
FIGURE 3.1
Typical cell and its important parts. This cell represents all types of cells, from the complex single-celled organisms such as amoebas to the cells in the human body. The ribosomes are the sites of protein synthesis. The mitochondria are the cells' energy factories, converting energy stored in nutrients into a form the cells can use to perform their various functions.

Continued in Figure 3.2.

Therefore, a sequence of codons codes for the linking together of amino acids to make a protein. This process is known as **protein synthesis**, which takes place outside the nucleus in the cytoplasm of the cell. (Protein synthesis and the entire genetic code are detailed in Appendix I.) For our purposes here, we will define *gene* in a functional way—that is, as that

protein synthesis The process by which the genetic code puts together proteins in the cell.

FIGURE 3.2
DNA molecule. This molecule is shown in the process of unwinding and copying itself prior to cell division (see Figure 3.3).


T
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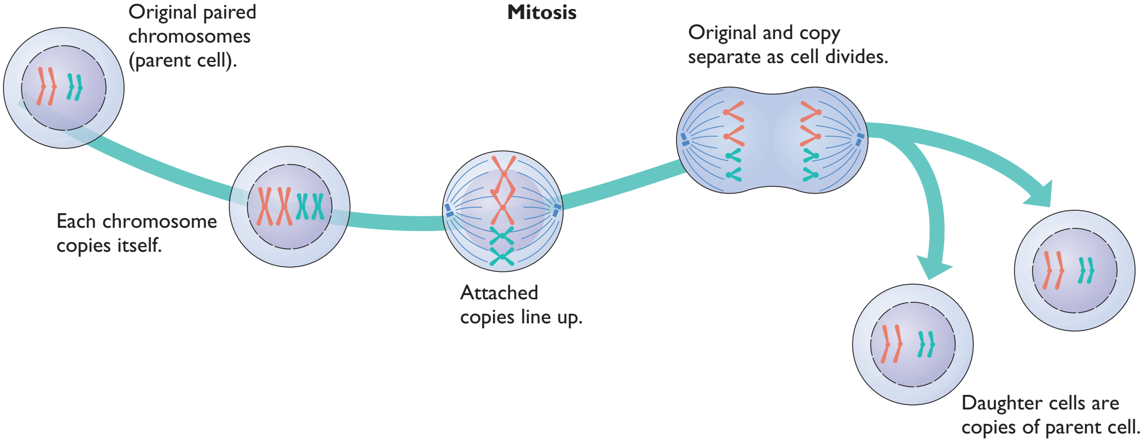

Original paired chromosomes (parent cell).
Mitosis
Original and copy separate as cell divides.
Each chromosome copies itself.
Attached copies line up.
Daughter cells are copies of parent cell.

FIGURE 3.3
The process of mitosis where exact copies of a cell are made.

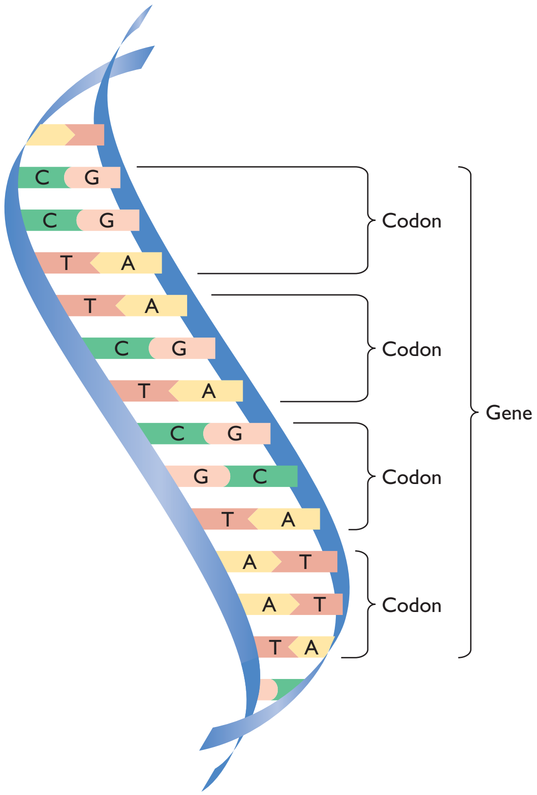


FIGURE 3.4
Section of DNA molecule with base pairs.

portion of the DNA molecule that carries the codon sequence for a particular protein (Figure 3.4).

It's still a long way from a protein to a trait—an observable, measurable physical or chemical characteristic of an organism. Some traits are fairly simple. Hemoglobin, the protein on red blood cells that carries oxygen, is made up of two chains of 141 and 146 amino acids. In other words, it is coded for by two genes—two sentences with 141 and 146 words.

Skin color, by contrast, is not a simple trait. It involves three different pigments and other factors such as skin thickness. The color of a person's skin is thus a trait produced by the complex interaction of many proteins and so is coded for on many genes. Such traits are called **polygenic** (Figure 3.5). Traits coded for by a single gene are called **monogenic**. Most traits of complex organisms are polygenic.

polygenic A trait coded for by more than one gene.

monogenic A trait coded for by a single gene.

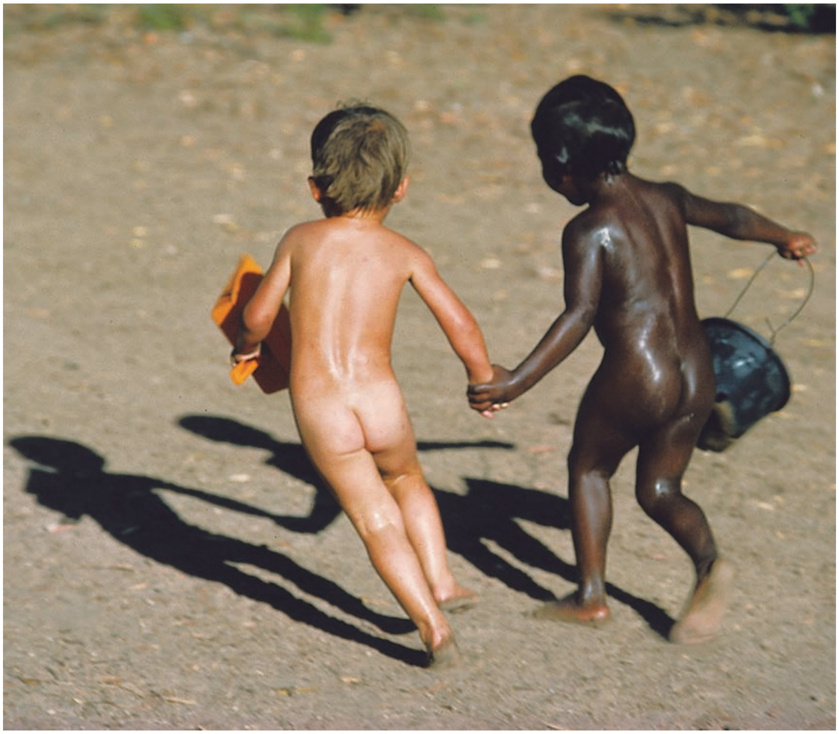


FIGURE 3.5
Skin color variation in humans is an example of a polygenic trait with a wide range of phenotypic expressions.

AN OVERVIEW OF THE HUMAN GENOME

As of spring 2003, nearly the entire human **genome** had been sequenced. What this means is that we knew the sequence of the 3.1 billion base pairs (the As, Ts, Gs, and Cs) of two representative humans' DNA. We then had a baseline from which scientists could further research the genome and compare people, populations, and different species.

There is still much to learn. We need to figure out just where in that 3.1-billion-base-pair sequence the genes are, what proteins they code for, what those proteins do. In other words, we still need to discover how the DNA "builds" an organism. But in the last few years, some remarkable new information has come to light.

genome The total genetic endowment of an organism.

It turns out that most of the genome is not composed of genes. That is, most of the genome—possibly 98 percent—doesn't code for proteins. We refer to this material as *noncoding DNA.* Although this DNA used to be referred to as "junk DNA," we now know that much of it serves a function. Some of it acts as punctuation, marking the beginnings and ends of coding sequences. Some of it regulates gene function and activity level. Some jumps around carrying other DNA with it, allowing the genetic code to reshuffle its elements, and some can occasionally become part of a gene. This provides a partial explanation for why a surprisingly small number of genes (25,000 by current estimates) can produce such a huge variety of proteins (around 90,000) in an organism as complex as a human being. Some noncoding DNA is made up of repetitive sequences, some hundreds of thousands of base pairs long, that may do nothing. Some of our DNA may be very ancient, from a remote common ancestor, and some may have been transferred from microbes.

Moreover, we have learned that coding sequences of a gene are not contiguous but are interrupted by noncoding sequences. The coding sequences can be spliced together in different ways to make different proteins. This is known as *alternative splicing* (Judson 2008). Indeed, each of our genes has, on average, three alternative versions (Ast 2005).

In addition, most amino acids are coded for by more than one codon. (There are only twenty amino acids but sixty-four possible codons—four bases in combinations of three, or $4^3 = 64$; see Appendix I for details.) It was previously thought that the particular "spelling" didn't matter so long as the same amino acid was the result. It turns out, however, that such differences, while producing the same protein, have other effects, such as changing how fast the protein is made and how much of a particular protein is made at a particular time (Judson 2008).

There are also many regulatory sections of DNA, found between and within coding genes. These may make up four times the space used by coding sections, that is, perhaps 4.5 percent of the genome. These sections have such functions as turning genes off when the correct amount of a protein has been synthesized, telling different cell types to use different versions of a gene, and affecting fetal development and nervous system functions.

Finally—and there are certainly more surprises to come—we now know that the chemical RNA, ribonucleic acid (see Appendix I), long thought to have just two forms that facilitated the process between the DNA code and protein building, comes in at least a half dozen other forms, which perform such functions as knocking out disease-causing genes, determining which genes are active and what proteins are produced, and turning genes off and on. (For a nice article on RNA see Pollack 2008.)

Thus, the nice neat view we've had of the genetic code and how it works, even until recently, has radically changed. In the words of Lewis

Carroll, the nature and operation of the human genome keeps getting "curiouser and curiouser" and will be an important area of study for years to come. (We'll return to and apply some of this new information in Chapter 13.)

FROM GENES TO TRAITS

If Mendel possessed neither the technology nor the background knowledge to understand DNA and the genome, what then did he discover about the processes of genetics? We refer to his contribution as **Mendelian genetics.** It involves the basic laws of inheritance, which we will take up in the next section, and some general principles about the relationship between the genetic code and the traits that are the end product of that code.

Mendel conducted at least eight years of extensive breeding experiments, the most famous on pea plants. He crossed plants that exhibited different expressions of a trait and then crossed hybrids with each other and back with the original plants.

Mendel used only traits that were monogenic (Figure 3.6). He carefully picked these after considering other traits, many of which were polygenic and so were rejected because, like skin color, they did not appear in simple either/or variation. While no modern scientists would simply leave out what didn't fit their expectations, we forgive Mendel because, in fact, all *genes* work the way he thought even if some *traits* are more complex.

Mendel reached the conclusion that each organism possesses two genes for each trait—one from each parent—and that these genes may come in different versions called **alleles.** Although Mendel used pea plants, it might be more interesting for us to use a human example. There is a chemical called PTC (phenylthiocarbamide) that people can either taste or not. (For those who can, it has a dry, bitter flavor. If you find brussels sprouts bitter, you are tasting a thiocarbamide.) This "taster trait" is monogenic, but the gene for the trait has two alleles: *T*, which codes for the ability to taste PTC, and *t*, which codes for the inability to taste the chemical.

Because we each possess two genes for the taster trait—one from our father and one from our mother—we each have one of three possible combinations. These combinations are called **genotypes.** We may have two of the same allele: *TT* or *tt*, a condition known as **homozygous** (from the Greek root *homo*, "the same"). Or we may have a pair of nonmatching alleles: *Tt*, a condition known as **heterozygous** (from the Greek root *hetero*, "different").

Mendelian genetics The basic laws of inheritance discovered by Gregor Mendel in the nineteenth century.

alleles Variants of a gene.

genotypes The alleles possessed by an organism.

homozygous Having two of the same allele in a gene pair.

heterozygous Having two different alleles in a gene pair.

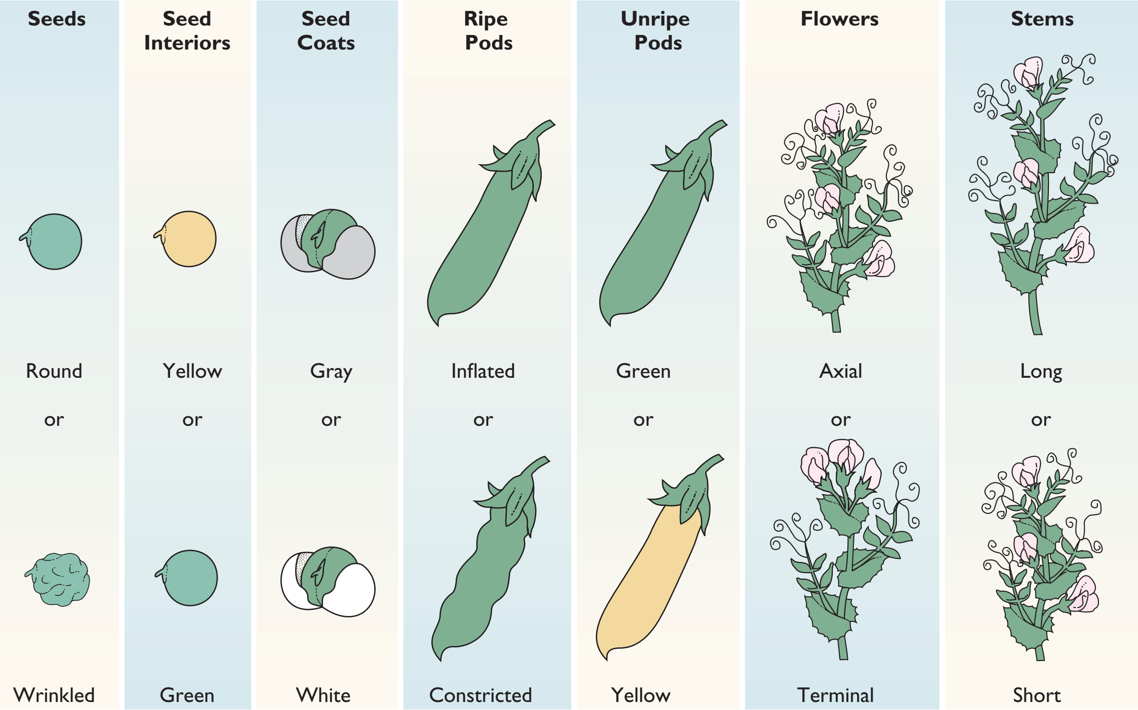

Seeds
Seed Interiors
Seed Coats
Ripe Pods
Unripe Pods
Flowers
Stems
Round
Yellow
Gray
Inflated
Green
Axial
Long
or
or
or
or
or
or
or
Wrinkled
Green
White
Constricted
Yellow
Terminal
Short

FIGURE 3.6
These are the traits of the pea plant that Mendel observed in his famous experiments.

These genotypes are responsible for producing the observable trait, the **phenotype.** What phenotype does each genotype produce?

Genotype	Phenotype
TT	Taster
tt	Nontaster
Tt	Taster

Why does the heterozygote *Tt* produce the same phenotype as the homozygote *TT*? Because, as Mendel also reasoned, some alleles are **dominant** and some are **recessive.** In this case, the allele for tasting is dominant (that's why it's written as a capital letter), and so, in the heterozygous genotype, it hides the action of the allele for nontasting. The only way a phenotype can reflect a recessive allele is if the genotype is homozygous for the recessive (*tt*).

phenotype The chemical or physical results of the genetic code.

dominant The allele of a heterozygous pair that is expressed in the phenotype.

recessive The allele of a pair that is expressed only if homozygous.

It is very important to understand that the words *dominant* and *recessive* have no value attached to them. Dominant alleles are not necessarily better or more common. There are, for example, quite a few human genetic diseases, some lethal, caused by dominant alleles. The terms *dominant* and *recessive* simply mean that if two alleles in this relationship are in a heterozygous genotype, the action of the dominant will be expressed and the action of the recessive will be hidden.

There is nothing magical about this. In the case of the taster trait, for example, the *T* allele codes *for* a protein that allows for the tasting of PTC and the *t* allele doesn't. Thus, the *T* shows up in the phenotype.

Alleles for most traits do not, in fact, work this neatly. In most cases, heterozygous genotypes result in phenotypes that exhibit some action of both alleles. (This is, in part, what led to the mistaken concept of "blending" inheritance.) Such alleles are said to be **codominant**, and they result in a greater number of possible phenotypes. In addition, many genes have more than two possible alleles, resulting in even more potential phenotypes. (Remember, however, that each individual can only possess a *pair* of alleles.)

A single example can demonstrate both these concepts. Your blood type for the ABO system is coded for by a single gene, the *I* gene, which has three possible alleles: I^A, I^B, and I^O. So we have six possible genotypes but only four possible phenotypes. (We can designate the genotypes using only the superscript, but remember that these are alleles of a single gene, not separate genes.)

GENOTYPE	PHENOTYPE
AA *AO*	type A
BB *BO*	type B
AB	type AB
OO	type O

It's clear that both *A* and *B* are dominant over the recessive *O*. The *AB* genotype, however, expresses the action of both alleles. The *A* and *B* alleles are codominant. (We will discuss the ABO system in greater detail in Chapter 12.)

There is a further complication, and it's an important one. The path between the genetic code and the resultant phenotypic expression can be influenced by outside factors, that is, factors that are not directly part

codominant When both alleles of a pair are expressed in the phenotype.

of the reading of the genetic code and the synthesis of proteins. We can call these nongenetic influences **environmental.** Certainly, some traits are unaffected by environmental influences. Your ABO blood type is a direct product of your genetic code—there's nothing that can change what those genes code for except a change in the code itself, a **mutation.** (We will discuss mutations in the next chapter.)

Other traits, however, are influenced by environmental factors. Your skin color, for example, is certainly coded for in your genes (there are at least four genes involved and probably more). Your specific skin color phenotype at any point in time, however, is influenced by a number of nongenetic factors: the amount of exposure to ultraviolet radiation from the sun, your health status, even your psychological condition (blushing from embarrassment, for example). In other words, two of us might have exactly the same genes for skin color but still differ in our phenotypic expression of that trait.

HOW INHERITANCE WORKS

Genes come in pairs. So do the chromosomes that carry these genes. Thus, the members of a pair of genes are found on a pair of chromosomes. Species differ in number of chromosomes. In humans, there are forty-six chromosomes, which come in twenty-three pairs (Figure 3.7). Chimpanzees have forty-eight chromosomes, wheat plants have forty-two, and dogs have seventy-eight. One species of amoeba has several hundred chromosomes.

When cells divide—as the organism grows or to replace cells—each chromosome copies itself. This process is known as **mitosis** (Figure 3.8). Some single-celled organisms reproduce in this fashion, but other single-celled organisms and nearly all multicellular organisms reproduce sexually, that is, by the joining of specialized cells from two parents. Such specialized sex cells are called **gametes** (sperm and egg in animals, for example). Now, if each gamete had a full set of chromosome pairs and thus a full set of gene pairs, the resultant fertilized cell—the **zygote**—and all the cells of the offspring, would have *twice* the normal number of chromosomes and *twice* the normal number of genes.

This duplication does not occur, however, because when gametes are produced, the chromosome pairs—and thus the gene pairs—separate. Mendel called this **segregation.** Each gamete, then, has only one member of each chromosome pair and so only one member of each pair of genes. The process of producing gametes is **meiosis** (Figure 3.8). When

environmental Here, any nongenetic influence on the phenotype.

mutation Any mistake in an organism's genetic code.

gametes The cells of sexual reproduction, which contain only half the chromosomes of a normal cell.

zygote The fertilized egg before cell division begins.

segregation In genetics, the breaking up of allele pairs in the production of gametes.

meiosis The process of cell division in which gametes are produced.

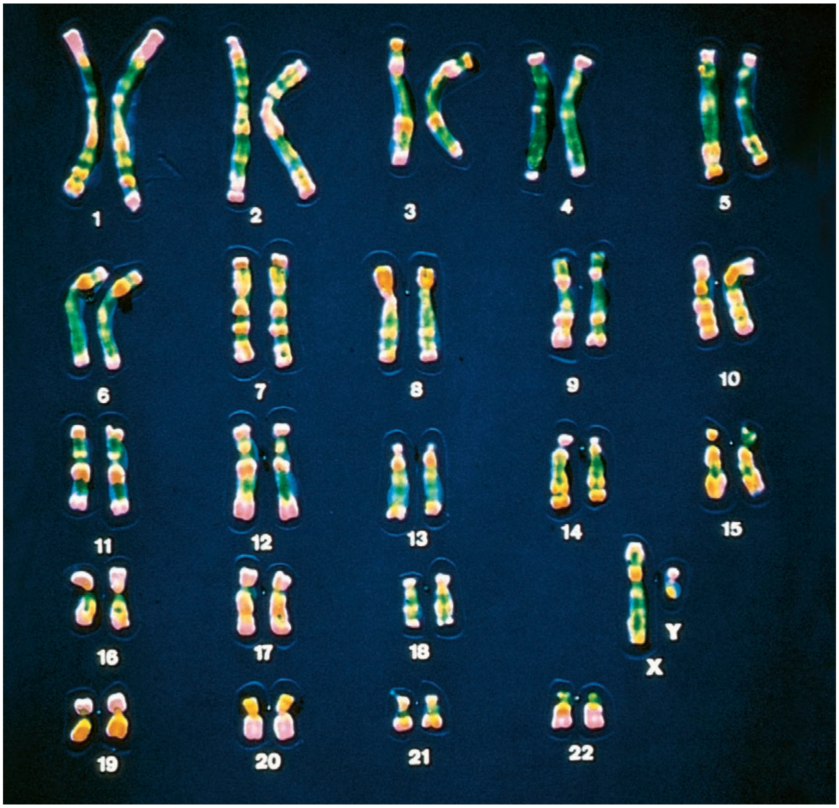


FIGURE 3.7
The twenty-three pairs of chromosomes typically found in a human being. This set of chromosomes came from a man—note the last pair has an X chromosome and a Y chromosome. A woman would have two X chromosomes.

the gamete from the male fertilizes the gamete from the female, the zygote once again has two of each chromosome and two of each gene. But because the members of each pair come from different parents, the combination of alleles for each gene may well be different from that of either parent.

We can demonstrate Mendelian inheritance using the taster trait. Suppose we have two individuals who are both phenotypic tasters and who are both heterozygotes, that is, their genotypes are *Tt*. Because chromosomes carrying allele pairs segregate during meiosis, each person will produce some gametes that receive the dominant allele and some that receive the recessive. At fertilization, then, depending on which sperm fertilizes which egg, three possible genotypic combinations are possible in the zygote. A device called a *Punnett square*, named after an English geneticist, illustrates this (Figure 3.9).

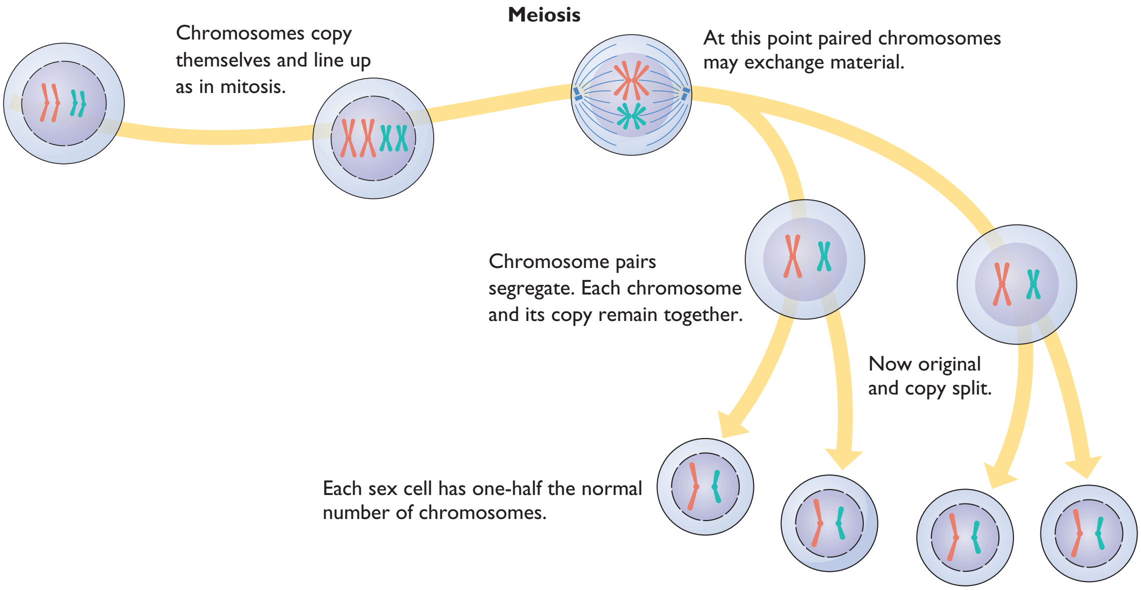
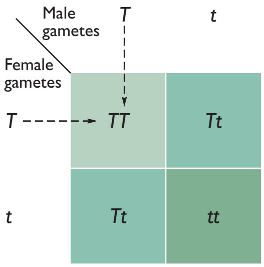

Meiosis
Chromosomes copy themselves and line up as in mitosis.
At this point paired chromosomes may exchange material.
Chromosome pairs segregate. Each chromosome and its copy remain together.
Now original and copy split.
Each sex cell has one-half the normal number of chromosomes.

FIGURE 3.8
Meiosis is the process by which gametes, or sex cells (sperm and egg), are manufactured. It ensures that when fertilization occurs, the new individual has a complete set of genes, one-half from each parent.

The cells of the Punnett square represent the possible fertilizations. If a *T* sperm fertilizes a *T* egg, the zygote is homozygous dominant. If a *T* sperm fertilizes a *t* egg, the zygote is heterozygous, and so on. Notice that two individuals with exactly the same genotype and phenotype can produce offspring with all three possible genotypic combinations and even, in the case of the homozygote *tt*, a different phenotypic expression. Two tasters, in other words, can give birth to a nontaster. This variation between parents and offspring is the result of the processes of segregation and fertilization. Variation is the raw material of evolution, the topic of the next chapter.

The Web site that accompanies this book includes a series of exercises that should add to your understanding of some of the topics covered in this book. The first is on Mendelian genetics as covered in this section.



Female gametes \ Male gametes	*T*	*t*
T	*TT*	*Tt*
t	*Tt*	*tt*

FIGURE 3.9
This Punnett square illustrates the possible genotypic combinations when two heterozygotes for the taster trait reproduce. Note that because of the hidden recessive, two tasters have a one-quarter chance of producing a nontaster offspring.

Contemporary Reflections

What Is Genetic Cloning?

Since advances in genetic technology enabled the cloning of Dolly the sheep in 1997, that ability and its potential applications have produced great scientific interest and heated controversy, much of the latter due to a poor general understanding of what the term *cloning* means. What immediately comes to mind are the plots from popular science-fiction novels and movies. For example, in Ira Levin's *The Boys from Brazil*, a Nazi scientist produces clones of Hitler, each, of course, with Hitler's personality.

Not only is something like that impossible, but it doesn't even come close to exemplifying the scientific meaning of cloning. The term *clone* simply refers to an exact or nearly exact copy of a biological entity, whether an individual or a cell. Identical twins, by that definition, are natural clones because they began life as a single fertilized egg cell and are, essentially, genetically the same.

In terms of artificial cloning, there are two main types and the distinction is important. Dolly and members of at least a dozen other species are examples of *reproductive cloning*. Here, the goal is the production of a genetic duplicate of an organism. Motivations range from increasing productivity of food animals to producing organs for transplantation to replicating pets. Not only are the functions of reproductive cloning open to ethical considerations, but at present there are severe limitations on its success, including the fact (probably mercifully) that it doesn't seem to work well with primates (Simerly et al. 2003).

Specific techniques differ, but in the most widely used method, the chromosomes are removed from an unfertilized egg shortly after ovulation, when it would be ready to develop if stimulated by the sperm. The donor cell, the one to be copied, is a somatic (body) cell, often a skin cell or a mammary cell. It is fused with the egg cell with the help of electric pulses, which also mimic the stimulation of fertilization. After about four or five days in a chemical solution, if all goes well, the fused cells will have developed into an embryo of several hundred cells. At this point the embryo is transferred to the uterus of a surrogate mother of the species in question, with the hope that it will develop normally. If it does, as was the case

SUMMARY

This brief account of the basic facts of genetics demonstrates two important points relative to evolution:

1. It is important to understand that all phenotypic traits are, initially, the products of the genetic code. Thus, evolutionary change is, at its most basic level, genetic change. But the pathway from the genetic code to phenotypic traits is a complex one. A gene simply codes for the synthesis of a protein. Proteins build cells, run their chemical reactions, link them together, and help them communicate; cells make up

with Dolly, the new organism will be an exact genetic copy of the individual from whom the donor cell was taken.

One misconception about this technique is that the clone will be a phenotypic duplicate of the donor. To be sure, clone and donor will be very much alike. But genes do not act alone in producing phenotypic traits, and many variables are involved in the path from single egg to multicellular organism. The more complex the trait, the more variable the potential results. So a clone of me would look something like me but would not have all my personality traits. Even if we could clone humans, we would not be making exact copies.

The second type of genetic cloning is *therapeutic cloning,* in which cells and eventually tissues are grown *in vitro* (in a chemical culture) for medical purposes. No reproduction of individuals is involved. The idea is to make copies of stem cells. These are cells, like a fertilized egg and cells from early in embryonic development, that have the potential to become all the different cell types in the body. In a few days, cells begin to specialize. At this stage (which is the same stage an embryo is implanted into a surrogate in reproductive cloning), certain cells are removed from the embryo in the hope of differentiating them into specific types of tissues to replace or repair a patient's tissue damaged by certain diseases, including Parkinson's disease, muscular dystrophy, and diabetes.

An objection to stem cell cloning is that an embryo—a potential life—is intentionally created only to be destroyed when the wanted cells are removed. But a new technique can "trick" an egg cell into "thinking" it has been fertilized so that it clones itself into an embryo. Such embryos are nonviable and could not lead to a pregnancy. In addition, there are stem cells still present in adult animals, and these could potentially be cloned and artificially differentiated. Ethical objections to therapeutic cloning seem easier to overcome than those to reproductive cloning, and the benefits to human health are of potentially inestimable value.

Both research and debate will continue on cloning, as well they should. But the former should be done with clear and beneficial goals in mind and the latter with sound, accurate knowledge of the science involved.

tissues, which in turn make up the body of a living organism—humans as well as pea plants. Moreover, this complex process is affected by environmental factors, so that the genetic code is most definitely *not* solely responsible for the final form and function of a living being. As we try to explain the phenotypic changes we see in evolution, we must keep these ideas in mind, for if the genetic process itself is complex, so, then, are the processes of evolution that act to change it.

2. The very process by which organisms pass on traits from parent to offspring also accounts for the variation seen between generations and among members of a species. If inheritance produced offspring that were exact copies of their parents, no change would ever take place and there would be no evolution—no adaptation, no change through time, and no new species.

QUESTIONS FOR FURTHER THOUGHT

1. New information about the specific nature of the human genome indicates, among other things, that we are, from several perspectives, not all that different from other organisms. We have far fewer genes than would be expected given our complexity. We share a great many of those genes with other organisms, from mice to bacteria. What philosophical issues might follow from these facts? How might these facts be applied practically?
2. We've considered some of the ethical concerns regarding cloning. How do you feel about the goals of reproductive cloning? Are they all equally worthwhile? What constraints should be placed on cloning? Should *any* reproductive cloning of humans be allowed? What about stem cell research? Do the same issues apply? Should companies be allowed to "own" certain lines of stem cells that came from a human and would be used to improve the health of other humans?

KEY TERMS

particulate
genes
proteins
amino acids
enzymes
chromosomes
deoxyribonucleic acid (DNA)
replication
mitosis
codon
protein synthesis
polygenic
monogenic
genome
Mendelian genetics
alleles
genotypes
homozygous
heterozygous
phenotype
dominant
recessive
codominant
environmental
mutation
gametes
zygote
segregation
meiosis

SUGGESTED READINGS

For a brief discussion of Mendel and an excerpt from his writing, see *Readings in the History of Evolutionary Theory* by Ronald K. Wetherington.

For the original announcement of the completion of the human genome, see the "Science Times" section of the 3 February 2001 *New York Times*, the 15 February 2001 issue of *Nature*, and the 16 February 2001 issue of *Science*. For a review of research since then, see "Initial Impact of the Sequencing of the Human Genome" by Eric S. Lander in the 10 February 2011 issue of *Nature*.

The topic of alternative splicing is covered in Gil Ast's "The Alternative Genome" in the April 2005 *Scientific American*, in "What Is a Gene?" by Helen Pearson in the 25 May 2006 *Nature*, and in "Inside the Code" by Olivia Judson in the March 2008 *Natural History*.

For more on our increasingly complex knowledge of how genes work, see "Regulating Evolution" by Sean B. Carroll, Benjamin Prud'homme, and Nicholas Gompel in the May 2008 *Scientific American*.

Some of the newly discovered complexities of the genome are covered in "The Inner Life of the Genome" by Tom Misteli in the February 2011 *Scientific American*; in "Evidence of Altered RNA Stirs Debate" by Erika Check Hayden in the 26 May 2011 *Nature*; and in "Shining Light on the Genome's 'Dark Matter'" by Elizabeth Pennisi in the 17 December 2010 *Science*.

Cloning technology is summarized in "Cloning for Medicine," by Ian Wilmut (who cloned Dolly), in the December 1998 *Scientific American*, with some new discussion in "A Decade of Cloning Mystique," by Jose Cibelli, in the 18 May 2007 *Science*.

4
CHAPTER
The Processes of Evolution

I am convinced that Natural Selection has been the most important, but not the exclusive, means of modification.
—Charles Darwin

One of the scientists who "rediscovered" Mendel's work in 1900 was the Dutch botanist Hugo de Vries (1848–1935). De Vries had been trying to explain the variations that sometimes spontaneously appear in plants (and, of course, in animals)—such as a single flower of the wrong color or one that is much smaller or larger than other members of its species. At that time breeders called these oddities "sports." De Vries called them *mutations*. When he read about Mendel's experiments, de Vries realized that these mutations resulted from sudden changes in Mendel's "factors." We now say that a mutation is any change in the genetic mechanism.

With de Vries's contribution, all the major pieces were in place to articulate the *synthetic theory of evolution*, which may be stated in the wonderfully concise phrase of Richard Dawkins (2005): Evolution is

the nonrandom survival of randomly varying hereditary instructions for building embryos.

In this chapter, we will explain Dawkins's statement and address the following questions:

What are species?

What are the processes of evolution?

How do these processes interact in the synthetic theory of evolution as we understand it today?

SPECIES: THE UNITS OF EVOLUTION

We observe evolution as the change in species over time and the development of new species. Evolution takes place in *populations* of organisms, and the basic population in nature is the species.

A species may be defined as *a population of organisms whose members can, under natural circumstances, freely interbreed with one another and produce fertile offspring*. Humans and chimpanzees, despite our genetic similarity, cannot interbreed and produce offspring, because our two species have different numbers of chromosomes. But any two normally healthy humans of opposite sex, no matter how different they may appear, can reproduce and generate fertile offspring. Thus, all human beings are members of a single species, *Homo sapiens*.

But it's not always so clear cut. Horses and donkeys can mate and produce offspring, known as mules. But mules are nearly always sterile. Two mules can't reproduce and make more mules. Thus, horses and donkeys are considered separate species that are unable to combine their genetic endowments for more than one generation.

Domestic dogs and wolves can and will mate and produce hybrid offspring that are fertile. Your family pooch is now lumped into *Canis lupus* and is, technically, a wolf, even though some breeds of dogs are so small that they could not mate with wolves, let alone carry and give birth to the fetuses of such matings (Figure 4.1).

If the species is the natural basic unit of evolution, then why is the distinction among various species sometimes so vague? Why aren't all species equally distinct? And why are scientists who specialize in classifying species (called **taxonomists**) sometimes at odds with one another over which populations belong to the same species? Coyotes and wolves, for example, can and do interbreed but, unlike dogs and wolves, they still are given different species names.

The answer to all these questions is that while the origin of new species from existing species usually happens relatively quickly, it does not happen instantly. Evolution is a *process* that takes place over time. Thus, there is usually a period when an emerging species still can interbreed with its ancestral species and is therefore difficult to define. For the moment, however, we will think of species as distinct, discrete units, and we will now describe those processes that produce evolutionary change within species and that, ultimately, bring about the origin of new species (the topic of Chapter 5).

taxonomists Scientists who classify and name living organisms.

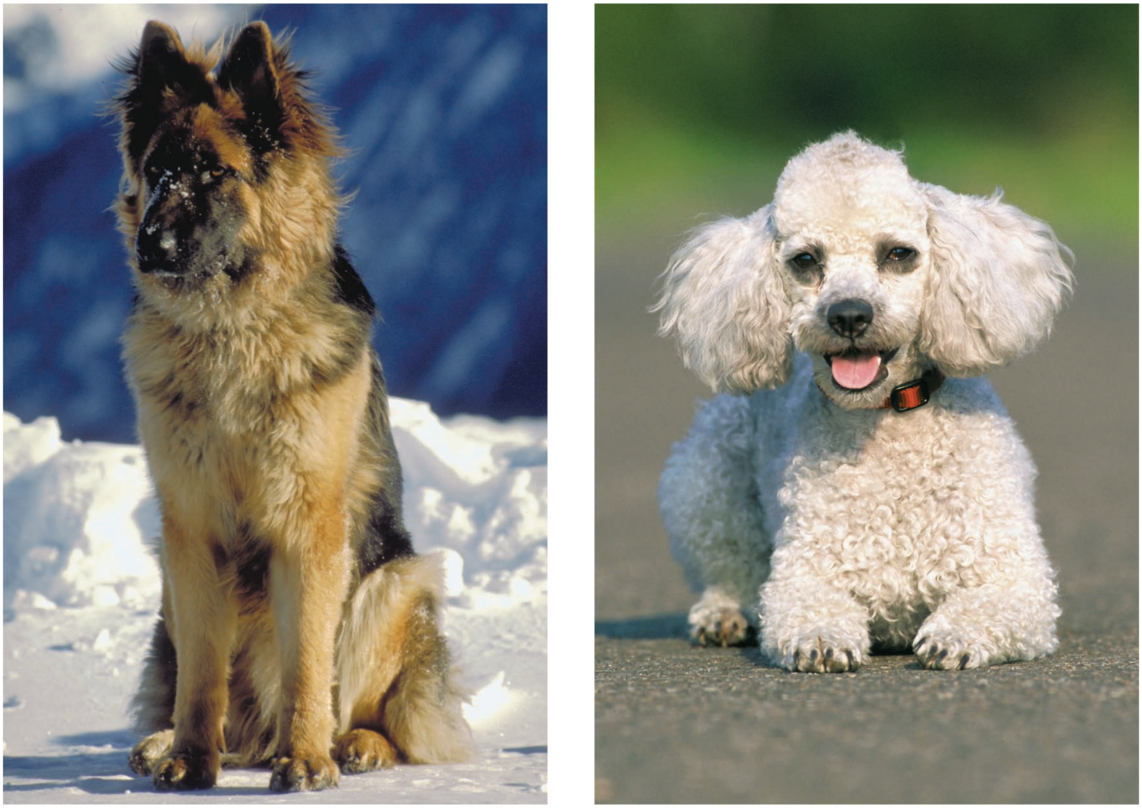


FIGURE 4.1
Wolflike and very unwolflike dogs. The German shepherd (*left*) closely resembles the wolf, an ancestor of all dog breeds. The miniature poodle (*right*) bears little resemblance to that ancestor. Both breeds, however, are genetically the same as wolves and could potentially interbreed with them.

THE FOUR PROCESSES OF EVOLUTION

Mutations: Necessary Errors

A mutation is any change in the genetic code. Some mutations involve a single incorrect base in a codon (one letter of one word). These are known as **point mutations.** Some point mutations are inconsequential, but some result in the wrong amino acid in a protein, which could have disastrous results for the organism. (An example is sickle cell anemia, a genetic disease, which we'll cover at the end of this chapter.)

point mutations
Mutations of a single base of a codon.

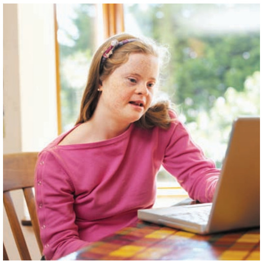


FIGURE 4.2
This child with Down syndrome has the characteristic facial features that are some of the multiple phenotypic effects of the presence of the extra chromosome 21.

Other mutations involve a whole chromosome or a large portion of one. These are called **chromosomal mutations.** They are almost always deleterious because many genes are involved. For example, humans who have three copies of chromosome 21, instead of the usual pair, have trisomy 21, or Down syndrome, which results in mental impairment and other phenotypic effects (Figure 4.2). This mutation most commonly results when a pair of parental chromosomes fail to segregate in the production of gametes.

Mutations are random. They occur continually, but exactly *what* mutation occurs is totally unpredictable. Some mutations are the result of environmental influences such as cosmic radiation, other forms of radioactivity, or chemical pollutants. Most, however, are simply mechanical errors that occur during the complex process of gene replication at cell division or during the even more complex process by which the genetic code is read, translated, and transcribed into proteins. They are occurring in the cells of your body as you read this sentence. Most affect just the individual, since they cannot be passed on. The process of aging, for example, is partly due to an accumulation of cells with mutations that make them in some way abnormal, though they are still alive and able to divide.

The only mutations that concern us in an evolutionary sense are those that occur in the gametes or in the specialized cells that produce gametes. These mutations are the ones that are passed on to future generations.

Because mutations are mistakes—deviations from the normal genetic code—mutations in coding regions are often deleterious. Such mutations produce a phenotypic result that is abnormal and therefore, to one degree or another, maladaptive. In other words, natural selection will select *against* those genes because their carriers won't be as reproductively successful. But mutations may also produce alleles that are neutral, making no difference to an individual's fitness, or they may produce alleles that result in even *better-adapted* phenotypes and are thus selected *for* by being passed on more often.

Mutation, in other words, adds genetic variation to a species' **gene pool.** Mutations are the price living things pay for the process of evolution. Without mutation—if the first life-forms had reproduced themselves absolutely without error—nothing would have changed, and the first living things would be the *only* living things. Mutations are thus one of the basic processes of evolution. They are necessary errors.

chromosomal mutations Mutations of a whole chromosome or a large portion of a chromosome.

gene pool All the alleles in a population.

Natural Selection: The Prime Mover of Evolution

By now, you should have a pretty good idea of how natural selection operates. Genetic variation within a species results in phenotypic variation. Much of a species' phenotypic variation may make little difference to the fitness and reproductive success of individuals.

Some phenotypic variation, however, *does* make a difference. How much of a difference, of course, depends on what traits are important for the adaptation of a particular species to a particular environment at a particular time. What's adaptive for one species—say, large size or a certain color—will not necessarily work for even a closely related species. As environments change, a trait that *was* adaptive for a species may no longer be adaptive, or a trait that was once neutral, or even nonadaptive, may now be adaptive.

Darwin's Finches Provide a Striking Example of Natural Selection in Action Rosemary and Peter Grant and their colleagues (Grant and

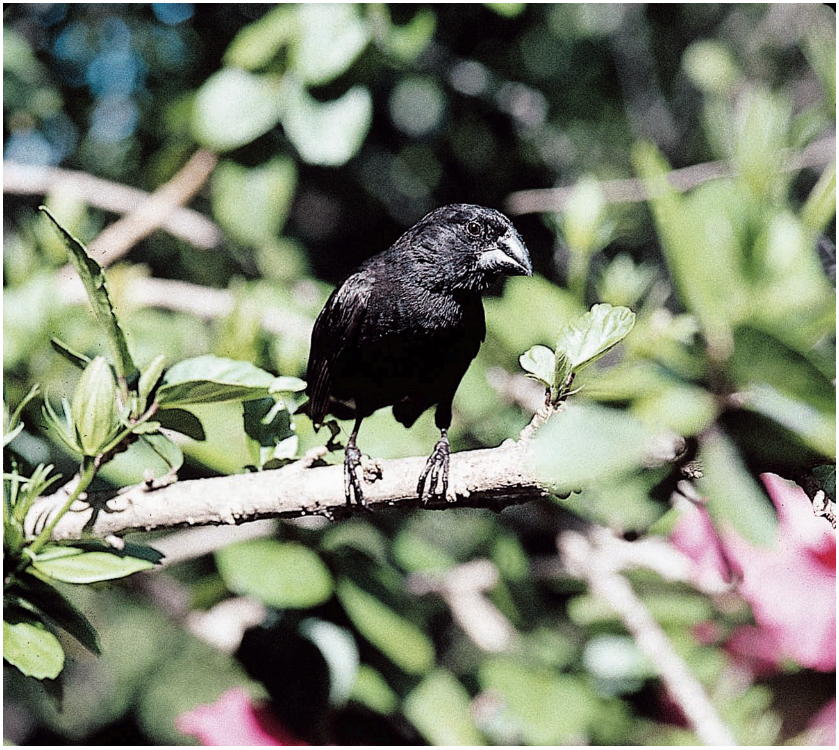


FIGURE 4.3
The medium ground finch, *Geospiza fortis,* was one of the species of Darwin's finches studied by Rosemary and Peter Grant and their colleagues.

Grant 2000, 2002, 2008; Weiner 1994) have studied the famous birds of the Galápagos Islands collectively known as Darwin's finches for over thirty years (Figure 4.3; see also Figure 5.3). Among the important adaptive features of these birds are their beaks, which have evolved to help each species of finch exploit particular food sources. In 1977 there was a severe and nearly yearlong drought on one of the small islands that the Grants' team was using as a study area. Insects virtually disappeared, and the only plant seeds available were larger than average and had tougher than average exteriors to preserve their moisture. The finches on the island suffered a serious food shortage.

The next year, when the rains returned, the researchers found that just one finch in seven (a mere 14 percent) had made it through the drought. The surviving birds of one species (the medium ground finch) were 5 to 6 percent larger than those that had perished and had beaks that were slightly (in fact, less than a millimeter) longer and deeper than the average before the drought. These are not big differences on a human scale, but the beak-size difference helped some of the finches crack open the larger, tougher seeds during the drought, enabling them to survive. As a result, many more males survived than females, because they are about 5 percent larger overall than females.

Now, however, because evolution takes place across generations, it had to be seen if this change would be passed on to the offspring of the surviving finches. This was, indeed, the case. It is the female finches who select males for mating. The males selected by the few surviving females were the largest and had the deepest beaks. As a result, the finches of the next generation were both larger and had beaks that were 4 to 5 percent deeper than the average before the drought. Moreover, when conditions, and thus food sources, returned to normal for a time, the average beak size decreased over several generations toward its previous dimensions. Larger beaks were no longer a distinct advantage and so were no longer selected for. These changes showed natural selection in action. Because of the severity of the situation, it took place rapidly enough for human observers to measure and record it.

There Are Two Important Implications of Natural Selection It is important to note that in the case of the finches, as in any example of natural selection, the variation that proved useful under changed circumstances was already present. It did not appear when it was needed or because it was needed. The finches that survived *already* had larger bodies and beaks; they did not develop these after the drought altered their food source. This is the essential difference between Lamarck's inheritance of acquired characteristics and Darwin's natural selection.

It follows that natural selection is not always successful in maintaining a species' adaptation and survival in the face of environmental change. If a change is too rapid or too extensive, the natural variation within a species simply may not be enough to provide any individuals with sufficient reproductive success to keep the species going. Natural variation within a species cannot predict what environmental change may take place in the future. Adaptation to change is a matter of luck. Indeed, for over 90 percent of all species that have ever existed, luck has run out; they are extinct.

Mutation and natural selection are the major processes of evolution. Mutation provides new genetic variation. Natural selection selects phenotypes for reproductive success based on their adaptive relationship with the environment. But because evolution is technically defined as genetic change, two other processes must also be considered as processes of evolution: gene flow and genetic drift (Figure 4.4).

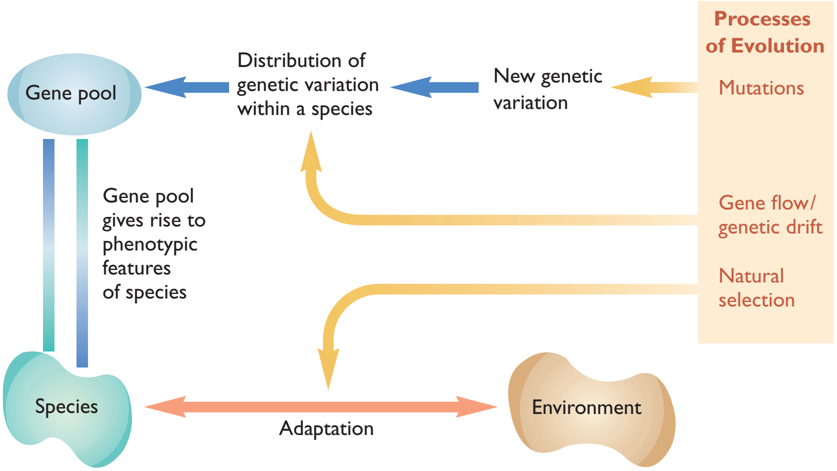

Processes of Evolution
Mutations
Gene flow/ genetic drift
Natural selection
Gene pool
Distribution of genetic variation within a species
New genetic variation
Gene pool gives rise to phenotypic features of species
Species
Adaptation
Environment

FIGURE 4.4
Processes of evolution. A species is in an adaptive relationship with its environment. This relationship is maintained by natural selection. Environments, however, are constantly changing, so the adaptive characteristics of a species change through time. In addition, the gene pool of a species is always changing, altering the phenotypes on which selection acts. Processes that alter a species' gene pool are also, by definition, processes of evolution. Mutation provides new genetic variation by producing new alleles or otherwise altering the genetic code. Gene flow and genetic drift mix the genetic variation within a species, continually supplying new combinations of genetic variables.

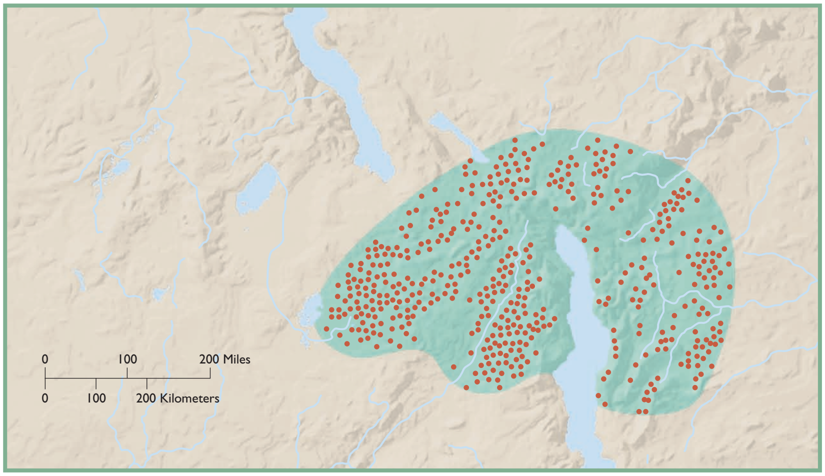


FIGURE 4.5
Breeding populations. The members of a species of lowland, nonaquatic animal (represented by the dots) are unevenly distributed within that species' range because of mountain and water boundaries. The separate population concentrations—the breeding populations—may show genetic and phenotypic differences.

Gene Flow: Mixing Populations' Genes

The members of a species are usually unevenly distributed over that species' range. Populations within a species can be to some degree separated from other populations by environmental barriers, geographic distance, or, in the case of our species, social and cultural distinctions such as political, religious, and ethnic boundaries. Such populations are called **breeding populations.** Individuals tend to find mates within their own breeding population (Figure 4.5).

Although belonging to the same species, breeding populations may exhibit genetic differences for two reasons. First, breeding populations may exist in somewhat different environmental circumstances from each other, as illustrated in Figure 4.5. Natural selection will have been favoring slightly different phenotypes in adaptive response to these environments.

Second, other genetic events (such as mutations and the evolutionary processes we're about to discuss) tend to be concentrated within breeding populations because that is where breeding is concentrated. What happens genetically in one breeding population will differ from what happens in another.

breeding populations Populations within a species that are genetically isolated to some degree from other populations.

gene flow The exchange of genes among populations through interbreeding.

However, because breeding populations *are* still members of one species, interbreeding between them does take place as populations and individuals migrate and as neighboring populations exchange genes. This is called **gene flow.** When members of different breeding populations interbreed, new genetic combinations are produced in the offspring. In other words, genes within a species "flow" among the populations of that species,

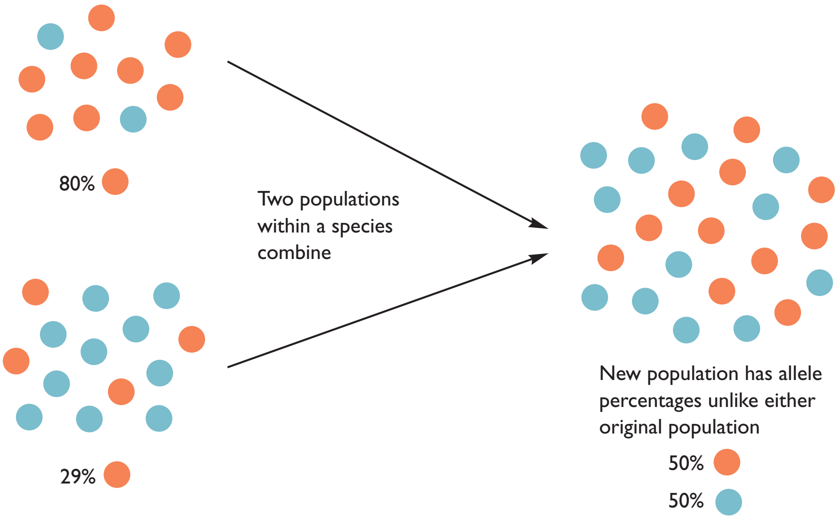


FIGURE 4.6
Simple example of gene flow where two populations merge. The dots represent the relative percentages of two alleles.

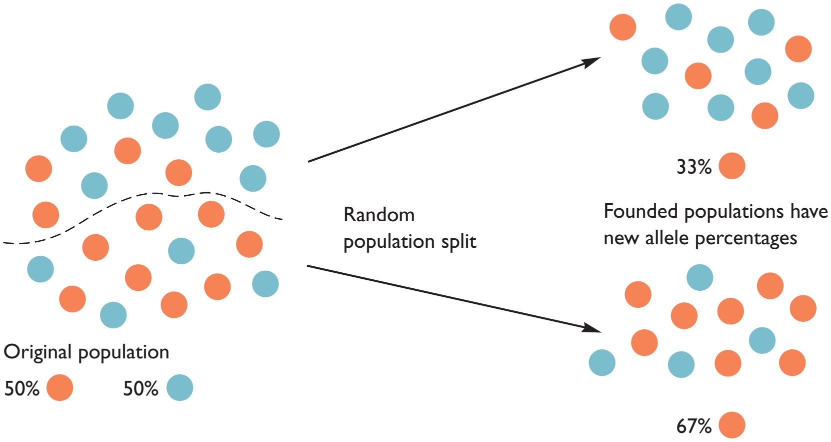
altering the distribution of genes and thus phenotypic variation of the species as a whole (Figure 4.6).

This process of evolution is particularly effective in a mobile species such as ours, with populations that are continually moving around and mixing genes. For example, about half of all Hutterite marriages (see Chapter 1) take place between colonies, with the bride moving to the colony of her husband. The woman thus brings her genes into the population and contributes them to subsequent generations. In one of the colonies I visited, 70 percent of the female parents came from other colonies, and marriages involving these women produced nearly 60 percent of the children of the next generation. Changes from one generation to the next in a Hutterite colony are greatly affected by this continual mixing, or flowing, of genes among populations, and it is the same for the human species as a whole.

Genetic Drift: Random Evolution

Fission and the Founder Effect One form of genetic drift can be demonstrated by the following experiment: Take 100 coins and arrange them so that 50 heads and 50 tails are showing. Mix them up and without looking (that is, at random) set aside 10 coins. The 10 coins you've chosen will probably *not* be 5 heads and 5 tails, 50 percent of each as in the original group. The odds are against it (about 4:1). Your sample of

FIGURE 4.7
Fission and the founder effect.



sampling error When a sample chosen for study does not accurately represent the population from which the sample was taken.

fission Here, the splitting up of a population to form new populations.

founder effect Genetic differences between populations produced by the fact that genetically different individuals established (founded) those populations.

bottleneck A severe reduction in the size of a population or the founding of a new population by a small percentage of the parent population that results in only some genes surviving and characterizing the descendant population.

10 will probably be a nonrepresentative sample, and this effect is called **sampling error.**

Similarly, when a population within a species splits, each new population will exhibit a nonrepresentative sample of the genes, and therefore the phenotypes, of the original. The splitting of a population is called **fission** (Figure 4.7). When one of the new populations is drawn from a small sample of the parental population, it will be strikingly different genetically (as with the coins above). This phenomenon is called the **founder effect.**

The Hutterites again provide an example. Because of their high birthrate—an average of ten children per family—colonies soon become so large that there are administrative problems and duplication of labor specialists. At this point, a colony will fission, or "branch out," as they put it. As a result, the three original North American Hutterite colonies, founded in 1874 and 1875, have become more than 380. As I saw in my study, these cases of fissioning and the founder effect had significantly altered the biological diversity among colonies.

In fact, the North American Hutterite colonies as a whole are an example of an extreme case of the founder effect. Only 300 Hutterites immigrated from Russia, and of those, only 90 contributed genes to future generations. Thus, most of the more than 38,000 present-day Hutterites trace their genes back to fewer than 100 ancestors. A founder population that comprises a small percentage of an original group is known as a **bottleneck.** In this case, the bottleneck was the result of the movement of a small number from one hemisphere to another. Other bottlenecks may result from an epidemic or a natural disaster.

The founder effect can have interesting and sometimes tragic results. In a population of 333 Pennsylvania Dutch, nearly one-third (98) were found to have the gene for Tay-Sachs disease, a fatal condition that kills recessive homozygotes by their fourth year of life (see also Chapter 14). The high frequency of this lethal recessive allele can be explained by the fact that these 333 people were all descended from one couple who founded the group in the nineteenth century. One of them, no doubt, by sad circumstance, carried the gene (Diamond 1991).

Fission, the founder effect, and gene flow are particularly important in the evolution of our species. They are processes caused by population movement, and our species is among the most mobile. We'll return to this topic in Chapter 13.

Gamete Sampling Another form of genetic drift is called **gamete sampling.** Just as genes are not sampled representatively when a population fissions, they are not sampled representatively when two individuals produce offspring. An organism passes on only one of each of its pairs of genes at a time, and only chance dictates which one will be involved in the fertilization that produces a new individual.

For example, refer back to the Punnett square of Figure 3.8, where two heterozygotes for the taster trait produce four children. Understand that those four possible genotypes are just *probabilities;* that is, two heterozygotes have a one-quarter chance of producing a homozygous dominant, a one-half chance of producing heterozygotes like themselves, and a one-quarter chance of producing a nontasting homozygous recessive. It's quite possible (the odds are 1 in 128) that they could produce four homozygous dominants; it all depends on what sperm fertilizes what egg:

$$\text{Tt} \times \text{Tt} \xrightarrow{\qquad\qquad} \text{TT, TT, TT, TT}$$

Note that the recessive allele has, just by chance, been completely lost. But what if another set of heterozygous parents produce four homozygous recessives? The effect is balanced:

$$\text{Tt} \times \text{Tt} \xrightarrow{\qquad\qquad} \text{tt, tt, tt, tt}$$

Combined, there is genotypic change but no overall genetic change. The four parents have 50 percent of each allele as do the eight offspring. No allele has been lost. Neither allele has gained in percentage.

gamete sampling The genetic change caused when genes are passed to new generations in percentages unlike those of the parental generation. An example of sampling error.

This is what might happen in a large population—the sampling error would be balanced. But in small populations, the size of a colony of Hutterites, for example, the change produced by one set of parents, such as in the first case above, would probably not be balanced by another set of parents.

The percentages of alleles, then, may change at random across generations, "drifting" in whatever direction chance takes them. The change may be great enough that certain alleles may be completely lost, while others may reach a frequency of 100 percent—all with no necessary relationship to natural selection based on the fitness of those alleles.

SICKLE CELL ANEMIA: EVOLUTIONARY PROCESSES IN ACTION

We can now take the ideas covered in Chapters 2 and 3 and see how they work in a real example. Sickle cell anemia is a genetic blood disorder; it is often associated with Africans and African Americans because it is found in high frequency in a band across the center of Africa. It is also found in North Africa, Southwest Asia, India, and Southeast Asia.

Genetics and Symptoms

Sickle cell anemia is the result of a mutation affecting hemoglobin, the protein on the red blood cells that carries oxygen from the lungs to the body's tissues. Hemoglobin is made up of two protein chains, one of 141 amino acids and one of 146. Mutations can occur anywhere in the genetic codes for these proteins, but if the codon in the sixth position of the longer chain mutates—one wrong word in a sentence of 287 words—an abnormal form of hemoglobin results (Figure 4.8).

When this abnormal form is present and stress, high altitude, or illness lowers an individual's oxygen supply, the red blood cells take on peculiar shapes, some resembling sickles (Figure 4.9). These misshapen cells cannot carry sufficient oxygen to nourish the body's tissues and can block capillaries. Symptoms include fatigue, retarded physical development in children, increased susceptibility to infection, miscarriage, fever, and severe pain. Sickle cell kills about 100,000 people a year,

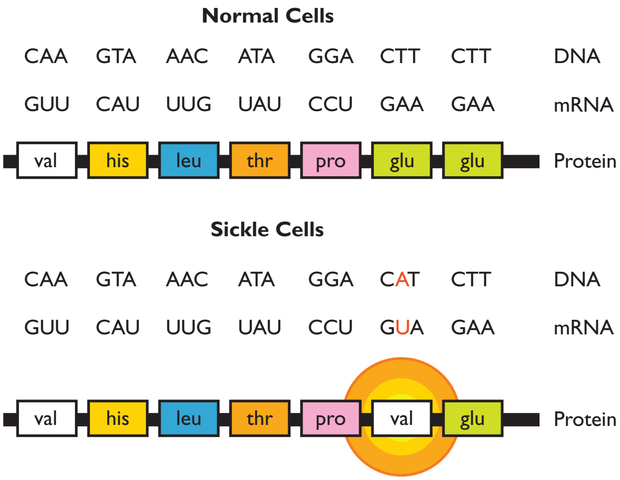

Normal Cells
CAA GTA AAC ATA GGA CTT CTT DNA
GUU CAU UUG UAU CCU GAA GAA mRNA
val his leu thr pro glu glu Protein
Sickle Cells
CAA GTA AAC ATA GGA CAT CTT DNA
GUU CAU UUG UAU CCU GUA GAA mRNA
val his leu thr pro val glu Protein

FIGURE 4.8
The mutation that causes sickle cell is one wrong base (A instead of T) in the sixth codon of the longer of the two genes. Valine instead of glutamic acid becomes the amino acid at that point and this results in an abnormal hemoglobin protein.

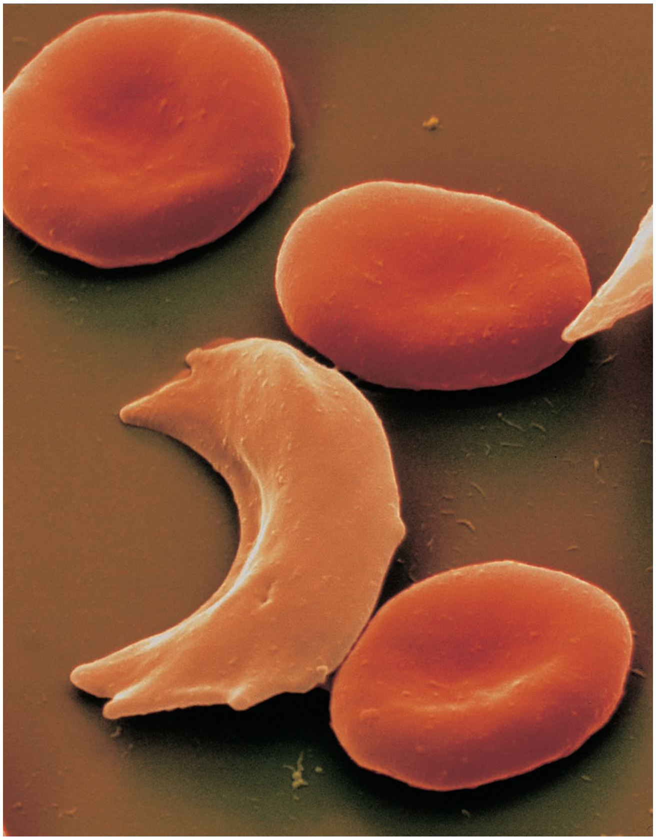


FIGURE 4.9
Normal red blood cells and one with the abnormal shape (*bottom left*) that results from the presence of hemoglobin with one incorrect amino acid. Such cells fail to transport oxygen properly to the body's tissues.

Contemporary Reflections

Are Humans Still Evolving?

As asked by most people, the question has two meanings. Perhaps the most common refers to the direction of future human evolution; in other words, how will we look in so many millions of years? As our minds do more and more of our work—and our bodies do less and less—will we eventually be great big heads atop short, spindly bodies? (This is the image we are often given of aliens from more advanced civilizations. Think of *Close Encounters of the Third Kind, E.T.*, or *The X-Files*.)

The answer to the first meaning of the question is, obviously, who knows? Evolution is so complex, so dependent on multiple, interacting series of events, that there is really no way of predicting the evolutionary future of any species, especially ours, with its ability to control its behavior, the environment, and, indeed, its genes through culture. If we could take a time machine back to the Cambrian period 543 million years ago and look at its animal life (see Figure 6.5), made up mostly of primitive arthropods (ancestors of modern insects, spiders, and crustaceans), who would predict that a rare little wormy creature only about 2 inches long, called *Pikaia,* would be the earliest-known representative of the chordates, the important group of organisms now represented by fish, amphibians, reptiles, birds, and mammals (Gore 1993; Gould 1989)?

A second, more sophisticated meaning of the question concerns whether we humans have stopped our evolution by so controlling our environment that natural selection is no longer in operation, that genetic variation is no longer an important factor in reproductive success. There are two parts to the answer. First, as we discussed, there are processes other than natural selection that bring about genetic change from generation to generation in a species. Our control over our environment certainly won't halt the processes of mutation, gene flow, and genetic drift. Indeed, one might argue that we have

85 percent of whom die before their 20s. Those who live longer experience constant pain and have very low reproductive rates. In terms of evolutionary fitness—that is, reproductive success—sickle cell anemia may be considered nearly 100 percent fatal. (It should be noted that there have been breakthroughs in the treatment of this disease, including a means of repairing the message from the DNA so that it produces normal hemoglobin. Treatment, however, remains out of reach for most people suffering from the disease.)

The abnormal allele (*S*) for sickle cell is an example of a codominant allele. An individual who is homozygous for the allele (*SS*) will have sickle cell anemia. A heterozygote, who inherits one sickle cell allele and one allele for normal hemoglobin (*AS*) will possess about 40 percent abnormal hemoglobin. These people are said to have the sickle cell *trait*. In extreme conditions of low oxygen, they may experience symptoms of increased mutation rates through some of our environmental manipulations and that our increasing mobility makes gene flow ever more powerful. So, by its genetic definition, evolution will always be taking place in our species.

But have we buffered ourselves against natural selection? For some genetically based characteristics, yes, we have. Remember that fitness is measured against a particular environment. If, through culture, we change the environment, we then change the adaptive fitness of certain phenotypes and thus of the genes that code for them. If I had lived in, say, *Homo erectus* times (1.8 million to 100,000 years ago), I'd no doubt be dead by now. If my infected appendix hadn't killed me (which it would have), my nearsightedness would have prevented me from being a very effective hunter or gatherer. Our present environment, however, has available all sorts of techniques and devices to improve one's eyesight. I wear glasses and see my optometrist once a year, so my poor vision (which, for the sake of the example, we'll say has a genetic basis) does not put me at any survival or reproductive disadvantage. You can probably think of dozens of other examples.

We have not, however, completely eliminated all relevant genetic variation. There are plenty of genes for diseases that place severe, or absolute, limits on a person's ability to reproduce and thus pass on those genes. Tay-Sachs disease, for example, is lethal well before reproductive age. Sickle cell anemia lowers reproductive rates in the few individuals who live long enough to reproduce.

And let's end on a hypothetical note (keeping in mind my precaution about predicting future evolution). There could well be some genetic variables that will make some difference in reproductive success in the near future. Suppose there is genetically based variation in humans' abilities to withstand less-than-optimal air quality or severely crowded living conditions or high levels of noise pollution. As these conditions worsen, it is certainly conceivable that genes for such tolerances will become more frequent as their possessors become less reproductively affected by the modern environment.

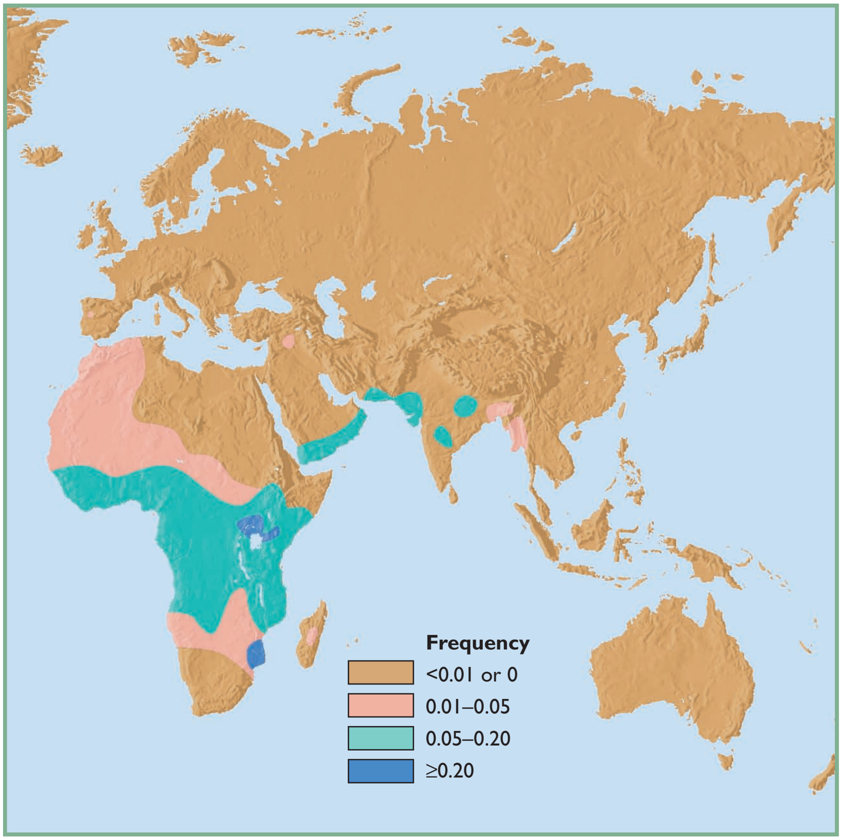
the disease but usually not as severe as homozygotes and with a great deal of variation from person to person. The heterozygous condition is not normally fatal.

For a disease that kills its victims, usually without allowing them to pass on their genes, sickle cell is found in unexpectedly high frequencies in parts of the world (Figure 4.10), in some areas as high as 20 percent. One would expect such an allele to be selected against and to virtually disappear.

The Adaptive Explanation

The answer to this puzzle is a perfect example of the complexity of natural selection. Not only do heterozygotes experience less severe episodes of the

FIGURE 4.10
Distribution of frequencies of the sickle cell allele. Compare this with the map of endemic malaria (Figure 4.11).



disease, they also have a resistance to malaria, an often fatal infectious disease caused by a parasitic single-celled organism and transmitted by mosquitoes. Malaria, though now treatable, still infects over 400 million and kills perhaps 3 million people a year, mostly African children younger than 5. Red blood cells with abnormal hemoglobin (recall that heterozygotes have about 40 percent of these cells) take on abnormal shapes when infected by the malaria parasite and die, thus failing to transport the parasite through the body.

Sickle cell is thus found in highest frequencies where malaria is found in highest frequencies (Figure 4.11) because heterozygotes are the healthiest in such environments and thus are relatively more successful at passing on their genes. Whenever two heterozygotes mate, they stand a one-quarter chance of producing an individual with normal

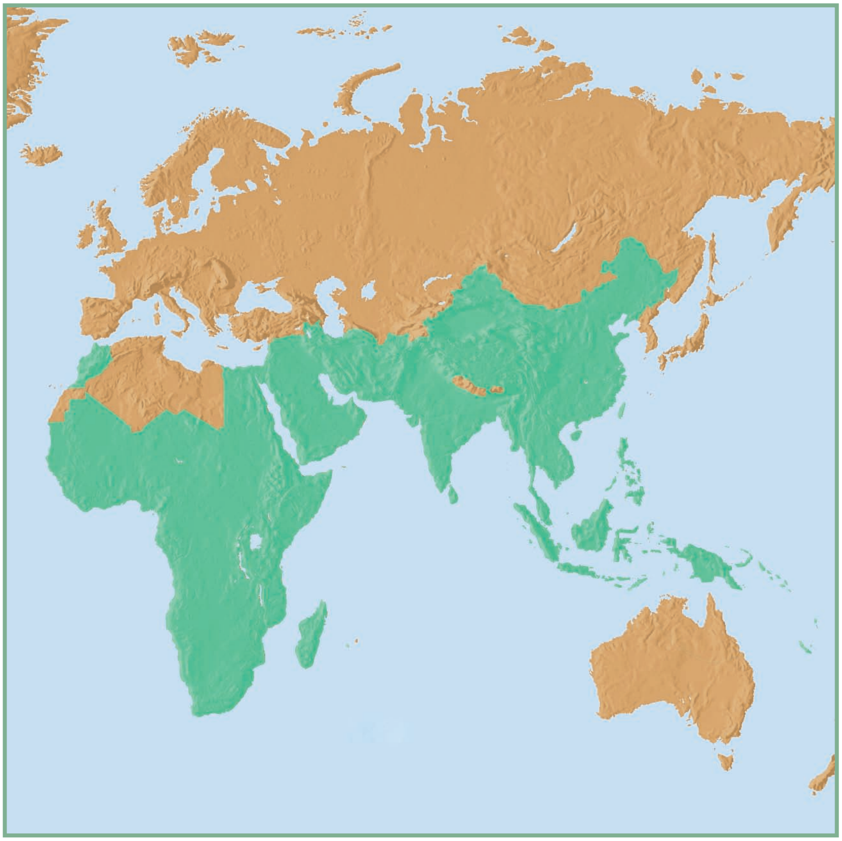


FIGURE 4.11
Distribution of endemic (consistently present) malaria. Compare with the map showing high frequencies of the sickle cell allele (Figure 4.10).

hemoglobin, a one-quarter chance of producing an offspring who will die from sickle cell, and a one-half chance of producing an offspring who will die neither from sickle cell nor from malaria but who will possess one sickle cell allele that can be passed on (Figure 4.12). This shows dramatically how adaptive fitness is related to specific environmental conditions. Even a potentially lethal allele may be adaptive under certain circumstances. In non-malarial areas there is no advantage to having an allele for sickle cell.

Other Relationships

The connection between sickle cell and African Americans is an example of the founder effect. African Americans can trace most of their ancestry

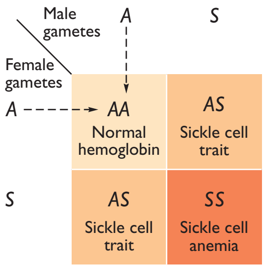


FIGURE 4.12
Punnett square for sickle cell anemia, showing the potential offspring of two heterozygotes. Because heterozygotes have an adaptive advantage in malarial areas but stand a one-quarter chance of producing an offspring with sickle cell anemia, the allele for sickle cell is maintained and passed on in such populations and the disease exhibits high frequencies.

back to the populations from West Africa that provided much of the slave trade to North America. The African American population was thus, in part, founded by individuals from an area where sickle cell already existed in high frequencies.

But sickle cell is less frequent among African Americans than it is among certain populations of Africans. This can be explained partly as a result of gene flow. There has been a good deal of genetic mixing between European Americans and African Americans over the past several hundred years. The addition of European genes would have lessened the frequency of the sickle cell allele in African Americans, because Europe is largely free of the disease since malaria is rare there. The presence of the disease among a small number of persons of largely European descent might be the result of their having an ancestor of African descent who carried the allele. Of course, the mutation that produces the sickle cell allele can occur in people of any geographic or ethnic background, European Americans included.

Moreover, because malaria is less common in the United States and Canada than in central Africa, there has been less of an adaptive advantage in possessing the sickle cell trait. Natural selection has thus been producing lower frequencies of the sickle cell allele, even in persons whose ancestors are from one of the areas of highest frequency.

Finally, there is evidence (Livingstone 1958; Pennisi 2001; Relethford 2003) that the frequency of malaria increased when people began farming in Africa several thousand years ago. Clearing and planting the land provides the sunlight and the pools of stagnant water that are ideal breeding grounds for the mosquitoes that carry the malaria parasite. An increase in malaria would result in increased selective pressures for the sickle cell allele, which, in heterozygotes, confers an immunity to the infectious disease.

Thus, the full story of this disease shows the interaction of the forces of evolution and involves not only genetics but also a single-celled parasite, an insect, and human demographic and cultural practices. The story of sickle cell is a perfect example of the holistic perspective of anthropology.

SUMMARY

To return to Richard Dawkins's brief definition of evolution, the modern theory begins with "randomly varying hereditary instructions for building embryos." This is the variation in a species' gene pool brought about by mutation, the mixing of genetic variation at reproduction, and the changes to the distribution of genetic variation from gene flow and the forms of genetic drift. Natural selection, then, involves "nonrandom survival," as individuals are more or less reproductively successful, thus accumulating adaptive phenotypes (and their genes) across generations and decreasing the frequency of poorly adapted traits (and their genes).

The basic unit of evolution is the species, an interbreeding population that is reproductively isolated from other populations. Because the evolution of new species is a process that occurs over time and at differing rates, species are not always equally distinct from one another and can often be difficult to define.

Sickle cell anemia is an example of not only the processes of evolution at work but also anthropology's holistic approach—the search for connections among the various aspects of its subject.

QUESTIONS FOR FURTHER THOUGHT

1. Domestic dogs are now classified in the same species as wolves, but humans have been able to produce through selective breeding hundreds of different dog breeds, each with its own phenotype and behavioral attributes—many decidedly unwolflike. Given what you know about the processes of evolution, how do you think we've accomplished this?
2. Severe bottlenecks can pose serious problems for species. We are seeing this now among cheetahs and elephant seals. What do you think the problem is with a severe bottleneck, in some cases even after the

species regains a fairly large population? Why is it actually threatening some species with extinction?

3. If I were an African American planning on having children, I might want to be screened to see if I were heterozygous for sickle cell. (I could be without ever having exhibited noticeable symptoms.) But since I am a European American, there is statistically little need for me to do so. Some people object to such reasoning, saying that it is potentially racist because it makes an assumption about one's health based on one's race. What do you think? Do you know of any other diseases that are statistically linked to certain populations?

KEY TERMS

taxonomists
point mutations
chromosomal mutations
gene pool
breeding populations
gene flow
sampling error
fission
founder effect
bottleneck
gamete sampling

SUGGESTED READINGS

A highly technical but very readable text on all aspects of evolution is *Evolution*, third edition, by Mark Ridley. The nature of species and the evolutionary processes that affect them are nicely covered in Edward O. Wilson's *The Diversity of Life*, a book about the importance of maintaining the biological diversity of the planet.

The research on Darwin's finches and the people who conducted it are the subjects of Jonathan Weiner's Pulitzer Prize–winning *The Beak of the Finch: A Story of Evolution in Our Time*. For an update, see Peter and Rosemary Grant's *How and Why Species Multiply: The Radiation of Darwin's Finches*. For what happened after the drought, see "Competition Drives Big Beaks Out of Business," by Elizabeth Pennisi, in the 14 July 2006 issue of *Science*.

For another informative example of the subtleties of natural selection in action, see "Why Do Cave Fish Lose Their Eyes?" by Luis and Monika

Espinasa in the June 2005 issue of *Natural History*. Also look at the entire November 2005 issue of that magazine.

For a discussion of the definition and origin of species, which also relates to the next chapter, see Stephen Jay Gould's article "What Is a Species?" in the December 1992 issue of *Discover*. See also the article of the same name by Carl Zimmer in the June 2008 *Scientific American*.

For more examples of natural selection among humans, see "Positive Natural Selection in the Human Lineage" by P. C. Sabeti et al., in the 16 June 2006 *Science*.

5
CHAPTER

The Origin of Species and the Shape of Evolution

Endless forms most beautiful and most wonderful have been, and are being evolved.
—Charles Darwin

The examples of evolution in action discussed in the previous chapter—the finches of the Galàpagos and populations of our own species interacting with malaria—focused on changes *within* single species. Darwin's book, however, was titled *On the Origin of Species*. What Darwin was ultimately trying to explain was how new species arise, the "mystery of mysteries" as he called it in his introduction.

We will address the following questions in this chapter:

How do existing species give rise to new species?

How do the processes of evolution contribute to the origin of new species?

How do species diversify?

What is the grand pattern of life's evolution?

NEW SPECIES

Species are, by definition, reproductively isolated from other species. Members of two species cannot mate and produce fertile offspring. Members of the same species can. What prevents interbreeding between species?

Reproductive Isolating Mechanisms

Any difference that prevents the production of fertile hybrid offspring between two populations under natural conditions is called a

reproductive isolating mechanism. These isolating mechanisms fall into several general categories (based on Dobzhansky 1970):

1. *Ecological adaptation*. Members of the populations are adapted to different environmental niches, even if their ranges overlap.
2. *Seasonal*. Reproduction within each population takes place at different times of the year.
3. *Sexual*. Behaviors that attract one sex to the other are different in the two populations.
4. *Mechanical*. The organs of reproduction (genitalia or flower parts) are incompatible.
5. *Different pollinators*. In flowering plants, different species, even if closely related, attract different insects, birds, or bats to facilitate pollination.
6. *Gamete isolation*. The cells of reproduction may be incompatible, thus preventing fertilization even if mating takes place.
7. *Hybrid inviability*. Fertilization may occur, but the hybrid zygotes do not survive.
8. *Hybrid sterility*. Hybrids survive but do not produce functional gametes.

The origin of new species, then, is the evolution of *any* of these differences between populations that prevent the production of fertile offspring. As biologist Edward O. Wilson puts it, "In order to spring forth as a species, a group of breeding individuals need only acquire *one* difference in *one* trait in their biology…. When that happens, a new species is born" (1992: 68; emphases mine).

How do such differences arise? It is important to understand that reproductive isolating mechanisms do not evolve *in order* to produce a new species. It is an accident when the differences in traits are isolating mechanisms. The differences themselves evolve through the processes of mutation, gene flow, genetic drift, and natural selection acting differently on isolated populations.

reproductive isolating mechanism Any difference that prevents the production of fertile offspring between members of two populations.

Processes of Speciation

Most Species Evolve in Separate Environments To take the simplest model, a species inhabits a wide geographic range, and populations at opposite ends of the range exhibit slightly different adaptive responses to

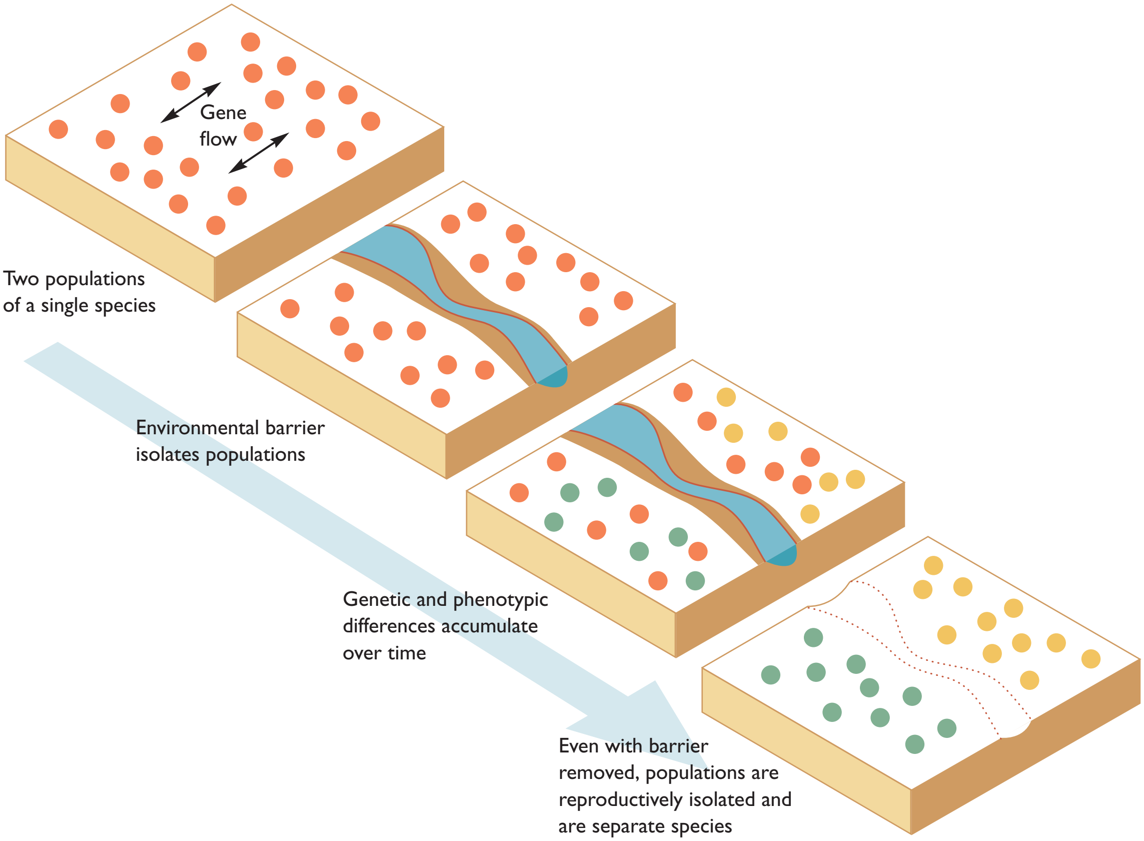

Gene
flow
Two populations
of a single species
Environmental barrier
isolates populations
Genetic and phenotypic
differences accumulate
over time
Even with barrier
removed, populations are
reproductively isolated and
are separate species

FIGURE 5.1
Simple example of speciation through environmental isolation.

particular environmental circumstances (Figure 5.1). Now, some environmental change—say, a river changing its course, the destruction of some important resource, or the advance of a glacier—splits the species, geographically isolating one population from another. Over time, each population will continue to adapt to its environment but without being able to exchange genes with the other population. In other words, there will be no gene flow. Each population will accumulate different genetic and phenotypic traits. Quite possibly one or more of these traits will, by chance, be a reproductive isolating mechanism. If at some later time the geographic barrier were removed and the two populations *could* mix, they would not be able to interbreed. They would be separate species, and we would say that **speciation** had occurred.

speciation The evolution of new species.

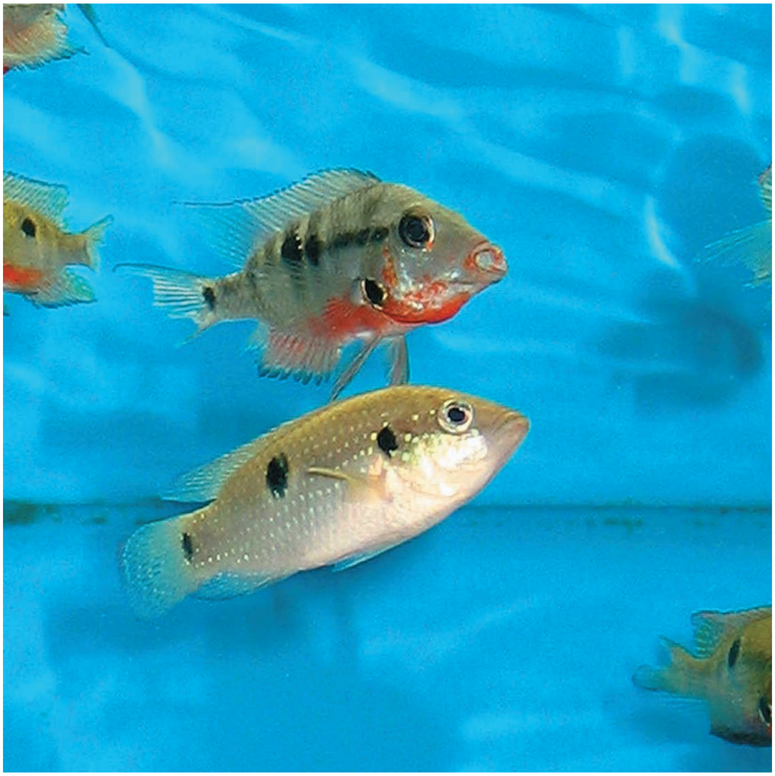


FIGURE 5.2
Two cichlids of different species, one from Central America and one from South America, illustrating the sometimes slight differences in color that the cichlids themselves respond to in mate selection.

Species Can Evolve within the Same Environment Even if there are no distinct geographic barriers separating portions of a species, speciation can still take place.

In a striking example, Johnson et al. (1996) have indicated that the basin of Lake Victoria in East Africa was completely dry only 12,000 to 14,000 years ago (ya*). And yet there are 500 distinct but closely related species of cichlid fishes in the lake, species found *nowhere else*. Clearly all these species have arisen fairly recently from, according to DNA studies, a single ancestral species. Apparently, cichlids are poor swimmers that prefer certain habitats and don't move around much. They may also have a tendency not to select mates outside their local group and to select mates according to color pattern (Figure 5.2). So small populations with, say, a new color resulting from a mutation, could quickly become isolated, and

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*By convention, I will use the following abbreviations throughout the remainder of the book: *ya* for "years ago," *mya* for "million years ago," and *bya* for "billion years ago."

this could account for what seems to be the world's fastest speciation rate in a vertebrate (Yoon 1996a).

Major Mutations Can Cause Speciation Occasionally speciation may be accelerated when a breeding population within a species shares a mutation with extensive phenotypic effects. Such mutations are called **macromutations.** Most macromutations are, as you would expect, deleterious. But by chance, some macromutations might be neutral or even beneficial. In such a case, they would be retained by natural selection, and they might serve to very rapidly make a small population within a species adaptively isolated from the rest of the species. Speciation is given a "head start" by the macromutation.

A relatively new area of study called *evolutionary developmental biology*—"evo-devo" for short—focuses on a special type of such mutations. Evo-devo is based on growing data suggesting that there are a small number of genes shared by all animals that control important steps in individual development (Orr 2005b). The same gene that triggers the development of eyes in fruit flies, for example, also does the same in mice.

But how do the same genes translate into such different phenotypes? Rather than resulting from an alteration in the proteins the genes code for, the phenotype is affected by *when* and *where* the genes are expressed, and this, in turn, is controlled by noncoding DNA, which acts as "switches" that turn specific genes on and off at certain times in certain cells. In other words, according to evo-devo, evolution is more a matter of mutations in this switcher DNA than in the coding genes.

The processes of evolution that bring about genetic and phenotypic variation are constantly in action (see Figure 4.4). So are the processes that alter environmental circumstances. It stands to reason, then, that the conditions that produce new species are ever-present and that speciation must be a very common occurrence indeed.

THE EVOLUTION OF LIFE'S DIVERSITY

Our Family Tree

No one is sure how many species of living things inhabit the earth, and we have no idea how many have *ever* lived on this planet. There are about 1.5 million *named* species living today; the total is certainly many times that number, possibly 100 million.

macromutations
Mutations with extensive and important phenotypic results.

Even in modern times, new species are still being discovered. In the 1990s, seven new monkey species were found in Brazil. Between 1999 and 2009 over 1,200 new species of animals were discovered in the Amazon. In about the same decade over 1,000 new species were discovered in New Guinea, and 200 new species were found there in a two-month period in 2010. A new seabird species was discovered just in 2011. New species of bacteria are being found by the thousands, including some recently discovered bacteria living in small spaces within rocks nearly 2 miles below the surface of the earth and at temperatures of more than 235°F.

Despite the great array of living creatures, however, there is a high degree of similarity among them all. All living things use the same genetic code; they are built from the proteins that are the products of that code, using the same basic twenty amino acids. We assume, then, that life on earth had a single origin. This being the case, all those millions upon millions of species have descended from a common ancestor and have come about by the process of speciation.

Adaptive Radiation

For a potential new species to persevere, it must survive the adaptive trials of natural selection. Put another way, it must have the ecological opportunity to be able to adapt to its environment. When such opportunities are extensive, speciation may take place numerous times, and a group of related species may spread into a number of niches. This spread of related species is called **adaptive radiation.** Evolution has been a story of the adaptive radiation of groups of species into different environments and the subsequent actions of the processes of evolution on those species.

Ecological opportunities come about and can foster adaptive radiation under three general circumstances:

1. When an environment supports no similar and therefore competing species
2. When extensive extinction empties a set of environments of competing species
3. When the new group of related species are adaptively **generalized** (as opposed to **specialized**) and are able to disperse successfully into different niches and displace species already there.

Here are examples:

adaptive radiation The evolution and spreading out of related species into new niches.

generalized Here, species that are adapted to a wide range of environmental niches.

specialized Here, species that are adapted to a narrow range of environmental niches.

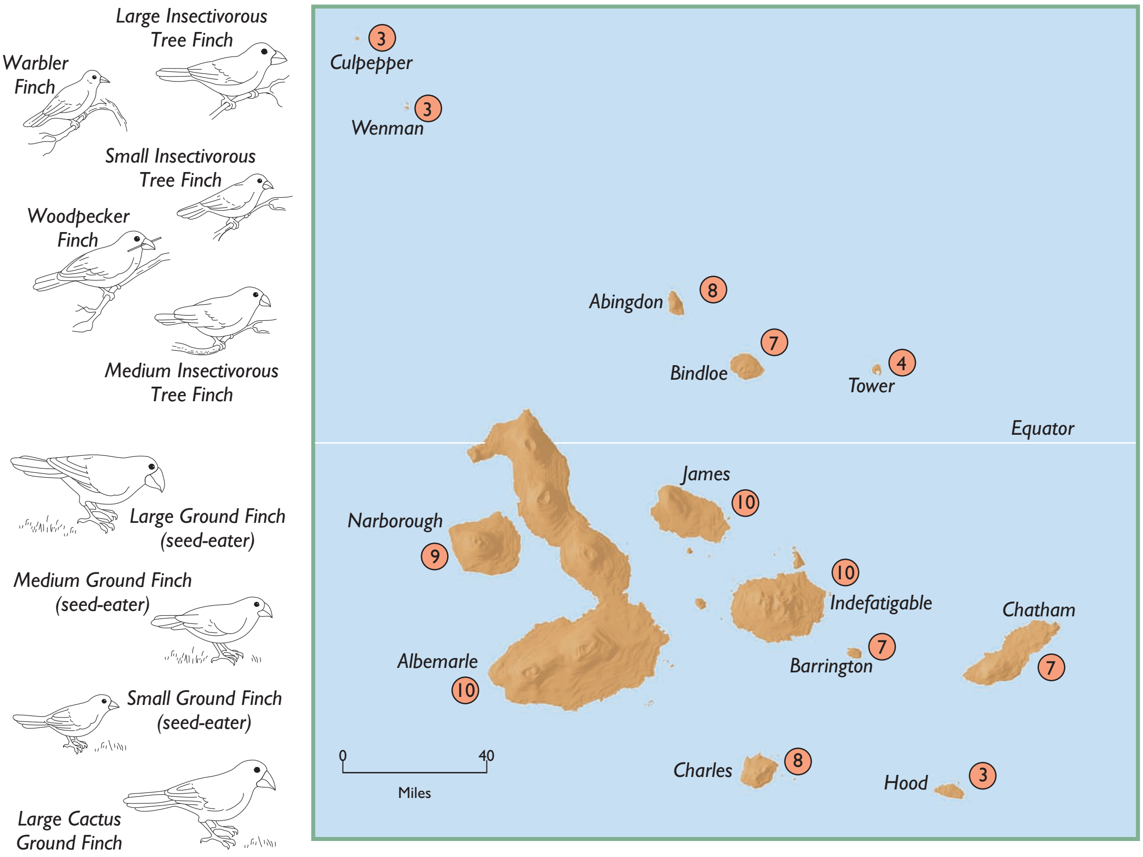

Large Insectivorous Tree Finch
Warbler Finch
Small Insectivorous Tree Finch
Woodpecker Finch
Medium Insectivorous Tree Finch
Large Ground Finch (seed-eater)
Medium Ground Finch (seed-eater)
Small Ground Finch (seed-eater)
Large Cactus Ground Finch
Culpepper 3
Wenman 3
Abingdon 8
Bindloe 7
Tower 4
Equator
James 10
Narborough 9
Indefatigable 10
Chatham 7
Albemarle 10
Barrington 7
Charles 8
Hood 3
0
40
Miles

FIGURE 5.3
The various species of Darwin's finches evolved when small groups from an original species underwent adaptation to the varying environmental conditions found throughout the Galàpagos Islands. The numbers on the map represent the number of finch species found on each major island. The bird drawings illustrate some of the variations observed among the species of Darwin's finches.

Darwin's Finches Had No Competition Darwin's finches (introduced in Chapter 4) are a group of thirteen related species that inhabit the Galàpagos, the volcanic archipelago of some nineteen islands in the Pacific about 600 miles west of Ecuador (Figure 5.3).

From a small group of original migrants of an ancestral species, blown out to the islands from the mainland of Central or South America no more than 3 mya, these birds have radiated into niches that were pretty much unoccupied by other birds. Today there are species of ground-dwelling finches that feed on seeds of different sizes and have bills shaped accordingly. There are several species that feed on cactus and several that live in trees and eat insects. One species is a tool-user, holding a cactus spine or twig in its bill and using it to probe for insects in tree trunks. The ground finches on two of the smaller islands peck the skin of larger birds and drink the surfacing blood. Not surprisingly, they are referred to as "vampire finches." There is

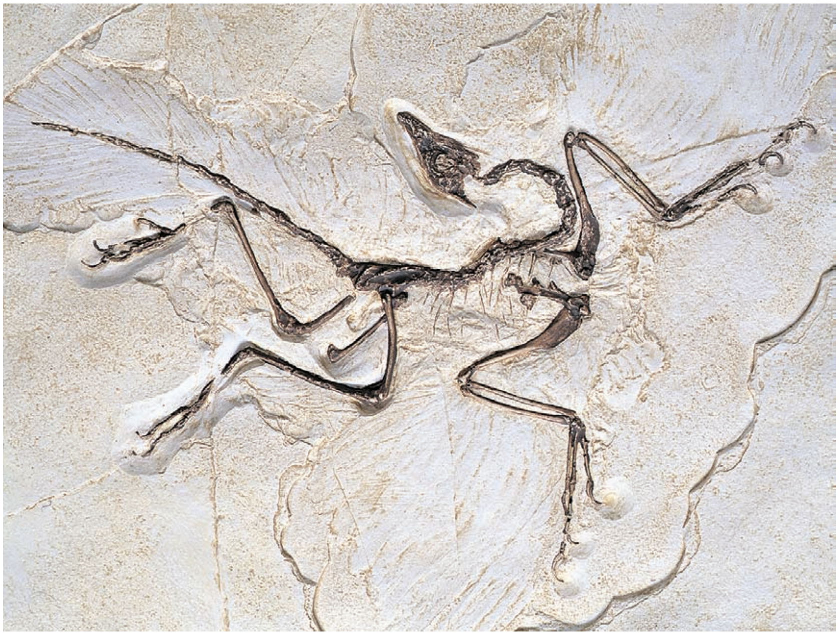


FIGURE 5.4
Fossil remains of *Archaeopteryx* ("ancient bird"), about 150 million years old. This is essentially a small bipedal dinosaur with feathers. The feathers, modifications of dinosaurian scales, are an example of an alteration in a species' genetic makeup that eventually gave rise to a whole new group of organisms.

new evidence that beak form influences the songs of the various finch species, which could also affect species distinction (Podos 2001).

In fact, birds in general are an example of adaptive radiation into empty niches. Birds first evolved some 150 mya from a group of dinosaurs (Figure 5.4). There was little competition for species possessing the new attributes of feathers and, for some, flight. This evolutionary novelty radiated into a wide variety of niches, resulting currently in about 9,000 species of birds of incredible diversity. All are variations on the same basic theme.

Mammals Benefited from a Major Extinction While mammals were already diverse during the time of the dinosaurs, the asteroid strike of 65 mya that killed off the dinosaurs and many other species opened up new niches for the survivors. The mammals (as well as surviving birds) radiated rapidly, and by about 40 mya the groups of mammals we recognize today had evolved.

The Primates Are a Generalized Group We can look to our own group of mammals, the primates, for examples of species that were able to radiate because they were generalized and could fairly easily disperse into diverse niches. When monkeys first evolved, about 40 mya, they proved more generalized than their **prosimian** ancestors, the earliest primates. The monkeys were larger-brained, **diurnal** (as opposed to the largely **nocturnal** prosimians), and well adapted to an active **arboreal** life, eating a mixed

prosimian A primate with primitive features, most closely resembling the ancient primates.

diurnal Active during the day.

nocturnal Active at night.

arboreal Adapted to life in the trees.

diet of leaves, fruits, and insects. As the monkeys underwent speciation and radiated into new niches, they displaced the prosimians. In the New World (Central, South, and North America), there are only monkeys (prosimians apparently became extinct in North America). In the Old World (Europe, Africa, and Asia), prosimians were pushed into marginal areas. A few species live on the mainland of Africa and the mainland of Southeast Asia, but most inhabit isolated islands of Southeast Asia and the island of Madagascar, which separated from mainland Africa prior to the monkeys' evolution (see Chapter 10 for more detail).

THE GRAND PATTERN OF EVOLUTION

In Chapter 4 we looked at evolution within species. This is known as **microevolution.** In this chapter we have looked at the basic level of **macroevolution,** the branching of new species from existing species. Now we want to finish with the overall pattern of the evolution of life—what does the tree of life look like, and what processes account for it? There are three important concepts that apply to this broadest level of macroevolution:

The Pattern of Speciation

One important idea we've already described: the origin of new species and, thus, the explanation for life's diversity, always involves the *branching* of new species from existing ones, in many cases with the original species continuing to exist. This is not always the common conception of evolution and, in fact, was not Darwin's conception. Common depictions of evolution (Figure 5.5) show it as linear change, one species changing so much it becomes eventually a new species. Darwin added to this a process whereby different varieties within a species diversify by natural selection, some becoming more successful and so "exterminating" the less successful varieties.

We now know it doesn't work this way. For one thing, if a single species—held together, you recall, by gene flow—changes through time, at what point does it become a new species? Where is the dividing line? Second, species tend to show stability during their tenure on earth. Changes occur but they are limited, taking place around the adaptive "theme" of the species. Recall the example of Darwin's finches and the drought from Chapter 4. When new species evolve it involves, as we've discussed, isolation of one or more populations within a species, with an interruption of gene flow. Thus, evolution is a thick, luxuriant bush with many branches. What appears in the fossil record to be straight-line change within individual

microevolution Evolutionary change within a single species through time.

macroevolution The branching of new species from existing species.

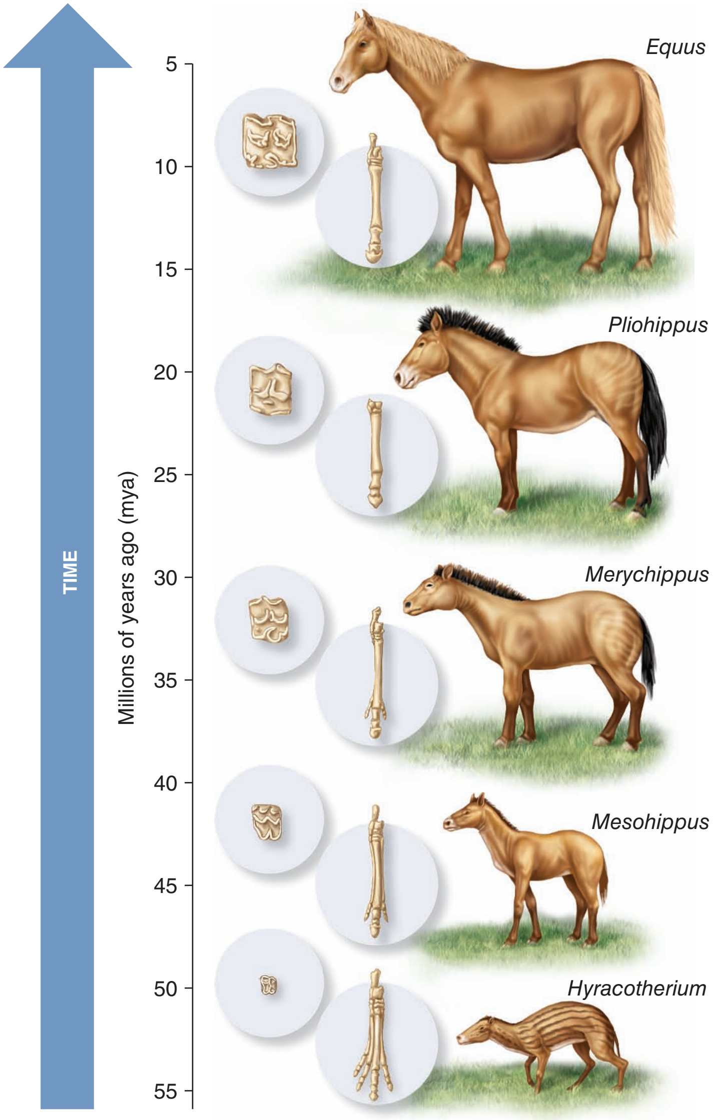

TIME
Millions of years ago (mya)
5
10
15
20
25
30
35
40
45
50
55
Equus
Pliohippus
Merychippus
Mesohippus
Hyracotherium

FIGURE 5.5
Traditional depiction of evolution, now discredited, as a linear progression, single species changing gradually through time.

punctuated equilibrium The view that species tend to remain stable and that evolutionary changes occur fairly suddenly through the evolution of new species branching from existing ones.

species is really a sampling of fossils from different branches (Figure 5.6). This is the concept known as **punctuated equilibrium.**

Species Selection

Darwin felt that selection took place only at the level of individual organisms competing for reproductive success, in other words, by natural selection as we've described it. But species may also compete with other species, but not necessarily directly as in natural selection among individuals. For example, some species may have traits that make them diversify into new species more rapidly than other species in the same environment. Thus, their descendants will eventually outnumber those of other species and will be more prominent, in living species and in the fossil record. The cichlids we described earlier, for example, are not necessarily better adapted to the East African lakes but are simply more prolific in branching into new species. This factor greatly influences larger patterns of evolutionary change through time.

Catastrophic Mass Extinctions

This is not the catastrophism of earlier centuries (see Chapter 2), that is, a long series of catastrophes that accounts for the entire geological and paleontological history of the earth. Nor does it contradict the general idea of uniformitarianism. It simply says that about five times in the history of our planet, some unpredictable and sudden environmental event brought about the extinction of large numbers of species, while others survived, and that these evolutionary changes were "nonselective" in the Darwinian sense. That is, species that became extinct may have been perfectly well adapted before the catastrophe but just couldn't survive it. They had, in the words of evolutionist Stephen Jay Gould, "bad luck" not "bad genes." Similarly, species that survived did so not because they suddenly adapted to the conditions of the catastrophe but because they *already* had adaptations that turned out, by luck, to be beneficial when the catastrophe hit.

As examples, we can look to the mass extinction of 65 mya (see Chapter 6 for details). All of the dinosaur species became extinct. They were doing quite well before the event, but no members of any of them had traits that allowed them to survive the major environmental changes brought about by an asteroid strike that set off a chain of worldwide calamities. Diatoms, however—a form of photosynthesizing algae and a major source of earth's oxygen—survived, while other forms of algae did not, because diatoms already had the ability to withstand adverse conditions because of their hard cell walls made from silica.

On a geological time scale, then, evolution is uniformitarian and gradual but species do arise relatively suddenly, species within the same environment do undergo a form of ultimate selection, and there have been a few major "glitches" in the history of life that reorganized the world's living things. All these have directed and redirected evolution as a whole, and we will see them all applied to the history of the primates and even to the human primate.

Contemporary Reflections

Are There Alternatives to Evolution?

All the information about the theory of evolution presented in Chapters 2, 3, and 4 has been developed and tested, using the methods and principles of science, over the past several hundred years by many people and from many different perspectives. Evolution is so well supported that we consider the basic idea to be a fact, and it is the central concept of all biology, although we continue to apply the scientific method to our investigation of specific details.

So it is truly astounding that some people, even today, question the fact that evolution has actually occurred, and many of these people base their questioning on religious belief. Why is this a problem? Think back to our discussion of science from Chapter 1. Science and belief systems are both important for the operation of any society, and, ideally, they operate in harmony with one another. They are still, however, distinct realms of knowledge, distinguished by the *testability* of science and the *faith* of belief.

But what about ideas that have characteristics of both? Suppose someone holds a scientific idea (an idea that is testable) but treats it as a belief by taking it on faith and by not recognizing the results of tests that refute it. Here's an example: there are people who believe that the lines on the palms of your hands and on your fingers hold information about your personal character and even, perhaps, about your future. This belief is called palmistry, and its precepts are quite scientifically testable. In fact, I examined them scientifically (Park 1982–83) and they failed. But will palmists all over the country close up shop because some anthropologist says their ideas are false? Hardly. Palmists take their ideas on faith. In other words, they treat a scientifically testable idea like a belief system. Thus, palmistry is a **pseudoscience,** or "false science."

Although pseudoscientific ideas such as palmistry, astrology, and the power of crystals may be harmless enough, other examples have implications that may not be so benign. Some pseudoscientific ideas find support within established belief systems. There are—believe it or not—still people who think the earth is flat and who refuse to acknowledge the masses of scientific evidence to the contrary (Schadewald 1981–82). This belief stems in large part from the literal interpretations of several biblical passages, for example, Matthew 4:8: "Again, the devil taketh him [Jesus] up into an exceeding high mountain, and sheweth him all the kingdoms of the world. . . ." How, the flat-earthers ask, could Jesus have seen all the kingdoms of the earth unless the earth were flat?

Although most people recognize the allegorical sense of this and similar passages in both testaments of the Bible, there is a danger that some might find the issue terribly confusing. On the one hand, scientific evidence—not to mention photographs taken from space—tells us unequivocally that the earth is a sphere. On the other hand, an interpretation of the chronicles of two major religions seems to say the earth is flat. Must one choose between science and religion? There are those who think so, and in the process, both science and belief suffer.

The idea of a flat earth is utterly ridiculous, but there is another pseudoscience, relevant to our topic here, that is far more complex and difficult to evaluate. It's called **scientific creationism.** It proposes that the entire universe, including the earth and all its inhabitants, was created spontaneously by untestable supernatural forces around 10,000 ya. Except for minor changes within "kinds" of plants and animals

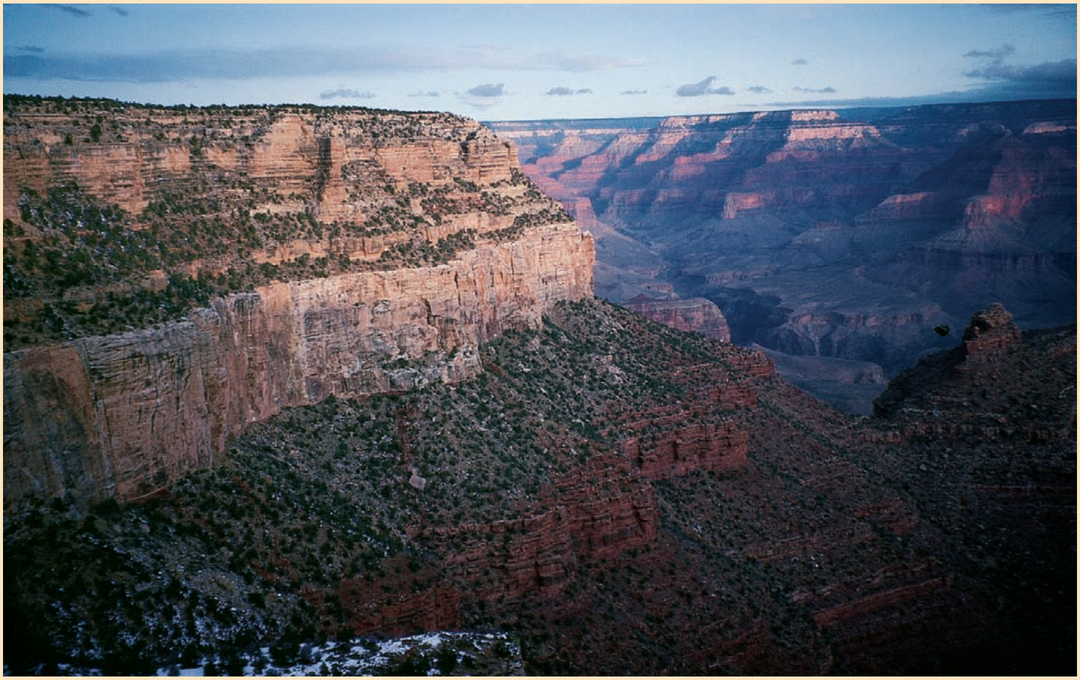


FIGURE 5.6
Strata of the Grand Canyon in Arizona. Scientific creationists contend that these strata and all the fossils they contain are the results of the biblical flood. Scientific data show that the canyon's strata represent geological and biological events that took place over nearly 2 billion years. (See also Figure 2.2.)

(breeds of dogs, for example, or regional varieties of a wild species), no changes in living organisms have occurred. Certainly no *new* species have arisen. But, we might ask, what about the layers of rock and soil and the fossils they contain? According to supporters of scientific creationism, those resulted from "a primeval watery cataclysm" (Morris 1974:22), a great flood in other words (Figure 5.6).

Sound familiar? It should. This argument derives directly from one literal interpretation of the first eight chapters of the book of Genesis, and it is clearly in direct opposition to all the data and ideas accumulated and tested by science. More than 200 years of scientific inquiry tell us that the universe, including the earth and its inhabitants, arose through knowable, natural processes. The universe is approximately 13 billion years old, the earth 4.5 billion years old, and life on earth roughly 3.6 billion years old. Living organisms do change through time, and species give rise to new species. The geological and fossil records are the records of these billions of years of change. We've been covering the evidence, data, and arguments for evolution in these last few chapters.

Scientific creationism is thus a pseudoscience—a testable set of ideas that even in the face of contrary evidence is accepted on faith. But scientific creationism goes further. Its proponents claim its ideas are, indeed, supported by scientific evidence that also refutes the accepted theory of evolution. That the creation model coincides with one interpretation of Genesis merely shows, they say, the scientific accuracy of the Bible. Because advocates of scientific creationism claim both models are scientific, they feel both should be taught in science classes as viable alternative explanations for the origin and diversity of life.

The argument is persuasive, especially in a society like ours, concerned with religious freedom and with our American sense of fair play and equal time. *But equal time is for equivalent things*. There is not a single shred of scientific evidence in support of the creation model.

To teach scientific creationism alongside evolution would be to violate the religious freedoms of those who do not subscribe to a strict creationist interpretation. It would also badly confuse those trying to learn how science really operates and what conclusions about our world science has arrived at. The distinction between science and belief would be blurred, interfering with the harmonious and important relationship between the two.

Recently, a new twist on this problem has surfaced with a new degree of complexity and, thus, a potential for unquestioned acceptance. It is generally referred to as **intelligent design.** It comes in several forms, but one will capture the idea. This version of intelligent design says that the basic chemistry of life—the cell, with its DNA, resultant proteins, and myriad reactions—is far too complex to have evolved naturally and so *must* have been designed by some intelligent entity. The more involved arguments use statistics to convey the great odds against putting together just the right combination of molecules that we now know are needed for life. Intimidated by such large numbers, many people accept the proposed improbability, if not impossibility, of life evolving by natural processes.

pseudoscience Scientifically testable ideas that are taken on faith, even if tested and shown to be false.

scientific creationism The belief in a literal biblical interpretation regarding the creation of the universe, with the connected belief that this view is supported by scientific evidence.

intelligent design The idea that an intelligent designer played a role in some aspect of the evolution of life on earth, usually the origin of life itself.

SUMMARY

The evolution of new species is the result of the interacting processes of genetic variation, natural selection, and environmental change. New species arise when a population within an existing species becomes isolated. Among the differentiating traits that result, some may act as reproductive isolating mechanisms, meaning that even if the populations once again have the opportunity to interbreed, they will not be able to do so. They will have become separate species.

The process of speciation, occurring countless times over the billions of years of life's history, has produced the incredible array of life-forms we know today and see in the fossil record. When species have the opportunity, they are able to adaptively radiate into new niches, and increased

There are two problems with this idea. First, the initial improbability of something happening doesn't *preclude* its happening. What was the probability at my birth that I would eventually become a biological anthropologist teaching at this university and, at this moment, writing a textbook? The answer is: infinitesimally small! And yet it happened, through all the contingent facts of my personal history—all the little things, many of them conscious decisions but many random, unpredictable, and accidental, which led to other things, and so on.

Similarly, for the evolution of life, a billion years or so passed from the formation of the earth to the first evidence of life (think of how long a billion years is). There are so many molecules, so many combinations of molecules to make compounds, so many individual chances for things to come together in different variations that we couldn't begin to even estimate the number. Among the things that did occur was the chemical combination, under just the right circumstances, that set in motion the chain of events that led to what we now call *life*. In other words, an intelligent designer is *not necessary*.

The second problem is that an intelligent designer is not a scientific (that is, testable) idea. The proposal of an intelligent designer based on supposed rational, scientific evidence (biochemistry and statistics) is just a thinly disguised version of scientific creationism. It ignores the majority of empirical evidence and substitutes an idea that cannot be tested, that *must* be taken on faith. There may well *be* some designer behind the universe we see, but a belief in such a designer is not a *substitute* for a scientific explanation of that universe.

The quality of our lives now and in the future depends on the continued progress of our testable scientific knowledge, mediated by the values of our belief systems. We need to understand what these two areas of knowledge are and how they interact, and we must promote free access to and sharing of all knowledge.

diversity is the result. It must be remembered, however, that all these forms are variations on the single theme of life that originated on this planet. All life, through speciation and adaptive radiation, is descended from a single origin.

The basic processes of microevolution (Chapter 4) and of speciation covered in this chapter are at the heart of the story of life on earth. But when we view the whole "pageant of life," macroevolution, we must expand on the basic theory. We need to remember that evolution is about branching of new species from existing species, with species remaining relatively stable throughout their tenure on the planet. In addition, species (or even larger units) undergo a form of selection, some persisting to branch into even newer groups, others dying out. Finally, life's history has been interrupted several times by catastrophic events that caused mass extinctions, events that radically changed the course of life's evolution.

QUESTIONS FOR FURTHER THOUGHT

1. Does the conflict between scientific creationism and mainstream evolutionary science mean that we must choose between science and religion? Are the two realms of knowledge, with regard to this subject, incompatible?
2. Consider the processes of evolution and speciation. Can you think of any examples of these processes in action today? How are human influences on the world part of these processes?
3. The result of adaptive radiation is biodiversity. Human actions are threatening the rich biodiversity of the planet. Is there a real problem with this, beyond the loss of some interesting or attractive species? How might diversity in and of itself be vital to the health of the planet?

KEY TERMS

reproductive isolating mechanism
speciation
macromutations
adaptive radiation
generalized
specialized
prosimian
diurnal
nocturnal
arboreal
microevolution
macroevolution
punctuated equilibrium
pseudoscience
scientific creationism
intelligent design

SUGGESTED READINGS

You should certainly have a look at the book that began our modern understanding of evolution, Darwin's *On the Origin of Species*. The last chapter, "Recapitulation and Conclusion," nicely summarizes his arguments and provides a good idea of his style. You can access the book at http://darwin-online.org.uk.

A wonderful book on evolutionary processes, the origin of new species, and the variety of living things is Edward O. Wilson's *The Diversity of Life*.

For more on Darwin's finches, see Jonathan Weiner's *The Beak of the Finch*.

A nice piece on the evo-devo model is "Turned On," by H. Allen Orr, in the 24 October 2005 *New Yorker*.

One of the originators of the model of punctuated equilibrium is biologist Stephen Jay Gould, and many of his articles concern that model. Try "The Episodic Nature of Evolutionary Change" and "Return of the Hopeful Monster," both in *The Panda's Thumb*. Gould has also addressed the shape of the evolutionary tree. See his informative books *Wonderful Life* and *Full House* and his article in the October 1994 *Scientific American*, "The Evolution of Life on the Earth."

For what many consider the last word on evolution, see Gould's magnum opus, his 1,433-page *The Structure of Evolutionary Theory*.

For an idea of the arguments of the scientific creationists, try *Evolution: The Fossils Say No!* by Duane T. Gish. For a refutation of scientific creationism, go once again to Stephen Jay Gould and a series of articles on the subject in *Hen's Teeth and Horse's Toes*. A good example of the intelligent-design argument is *Darwin's Black Box*, by biochemist Michael J. Behe. For a discussion, see the January–April 2002 issue of *Reports of the National Center for Science Education*.

See H. Allen Orr's article on intelligent design, "Devolution," in the 30 May 2005 *New Yorker*.

The National Center for Science Education, Inc. (NCSE) works to support the teaching of evolution and to increase public understanding of evolution and science. It publishes "Reports of the NCSE," which contain interesting and useful articles on all aspects of this topic. Its Web site is http://ncse.com.

The relationship between science and philosophical ideas, brought out so powerfully by the issue of scientific creationism, is addressed in Kenneth Miller's *Finding Darwin's God* and in Stephen Jay Gould's *Rocks of Ages;* for a very broad discussion, see *Consilience*, by Edward O. Wilson.

CHAPTER 6

A Brief Evolutionary Timetable

And there is no new thing under the sun.
—Ecclesiastes 1:9

Anthropology focuses on one group of organisms, humans and our direct ancestors, and deals mostly with a single species, *Homo sapiens*. Humans, in a broad, nontechnical sense, have been around for 5 or 6 million years. Depending on one's interpretation our species has inhabited the earth for 2 million years at most. Although this seems like a long time, it is really just the last tick of the earth's evolutionary clock, four-hundredths of 1 percent (0.04 percent) of the history of our planet, and one-hundredth of 1 percent (0.01 percent) of the estimated history of the universe. If the history of the universe were reduced to a single year, our species would not show up until after 11:30 p.m. on December 31.

Before we focus on ourselves, our close relatives, and our immediate ancestors, we need to put human evolution in context, to see it as part of a long and ongoing series of changes that began 13 bya.

Following are two questions we will consider in this chapter:

What is the history of the universe, the earth, and life on earth?

What processes and events have affected the overall history of the earth and life on earth?

FROM THE BEGINNING: A QUICK HISTORY

The origin of the universe is shrouded in mystery. We don't, in all honesty, really know exactly how old it is, although 13 billion years is the current estimate. We do know, however, that the universe is expanding in all directions. All the galaxies in the universe (an estimated 50 billion) are constantly traveling farther away from each other. The universe began as an incredibly tiny, dense, and hot speck (a *singularity*) composed of pure energy that would one day become all the energy and space and matter—including us—of the universe we know.

At the beginning of time—we'll use 13 bya—this speck began to expand, an event commonly called the Big Bang, although it wasn't really an explosion. It was more like a balloon being rapidly inflated—a balloon that contained both energy and space. The details of the Big Bang are still a matter of intense debate but for our purposes here, suffice it to say that as the newborn universe expanded, it cooled, and matter quickly condensed from energy (Figure 6.1). Within 3 minutes after the beginning, protons and neutrons had formed and had joined to make atomic nuclei, but it took another 100,000 years for electrons to join the nuclei to form atoms. At about the same time, radiation separated from matter and there was light, but for the next 200,000 years the universe was still too dense for that light to travel through it.

By 12 bya, galaxies had begun to form as gravity pulled matter together into huge clusters. These were made up of stars that were mainly hydrogen, the simplest element. As a result of the nuclear reactions in these stars, heavier, more complex elements formed. When these early stars died in tremendous supernova explosions, their elements were scattered into space, some eventually contributing to the formation of new galaxies with all their stars and planets. (Over 300 planets have been discovered orbiting other stars in our galaxy.)

About 5 bya, when the universe was two-thirds its present size, our solar system formed around a medium-sized star in the Milky Way galaxy. Earth, the third of eight existing planets orbiting that star, came into being 500 million years later. Amazingly, in less than a billion years—maybe 3.6 bya—life on earth was established. We know this indirectly from fossils found in Greenland, southern Africa, and Australia (Figure 6.2). In Australia there are also actual fossils, preserved in stone, of single-celled organisms from at least 2.7 bya, many of which were probably already capable of **photosynthesis.** This produced oxygen to about modern levels by 2.45 bya.

Just how life came about on the earth is also a matter of debate. Scientists have been able to produce carbon-rich **organic** compounds with a fairly simple laboratory procedure, showing that the process could have occurred quite easily. In fact, they have been able to produce

photosynthesis The process by which plants manufacture their own nutrients from carbon dioxide and water, using chlorophyll as a catalyst and sunlight as an energy source.

organic Molecules that are part of living organisms. They are based on the chemistry of carbon and contain mostly hydrogen, oxygen, carbon, and nitrogen. Even carbon-based molecules that are not found in living things are sometimes referred to as organic.

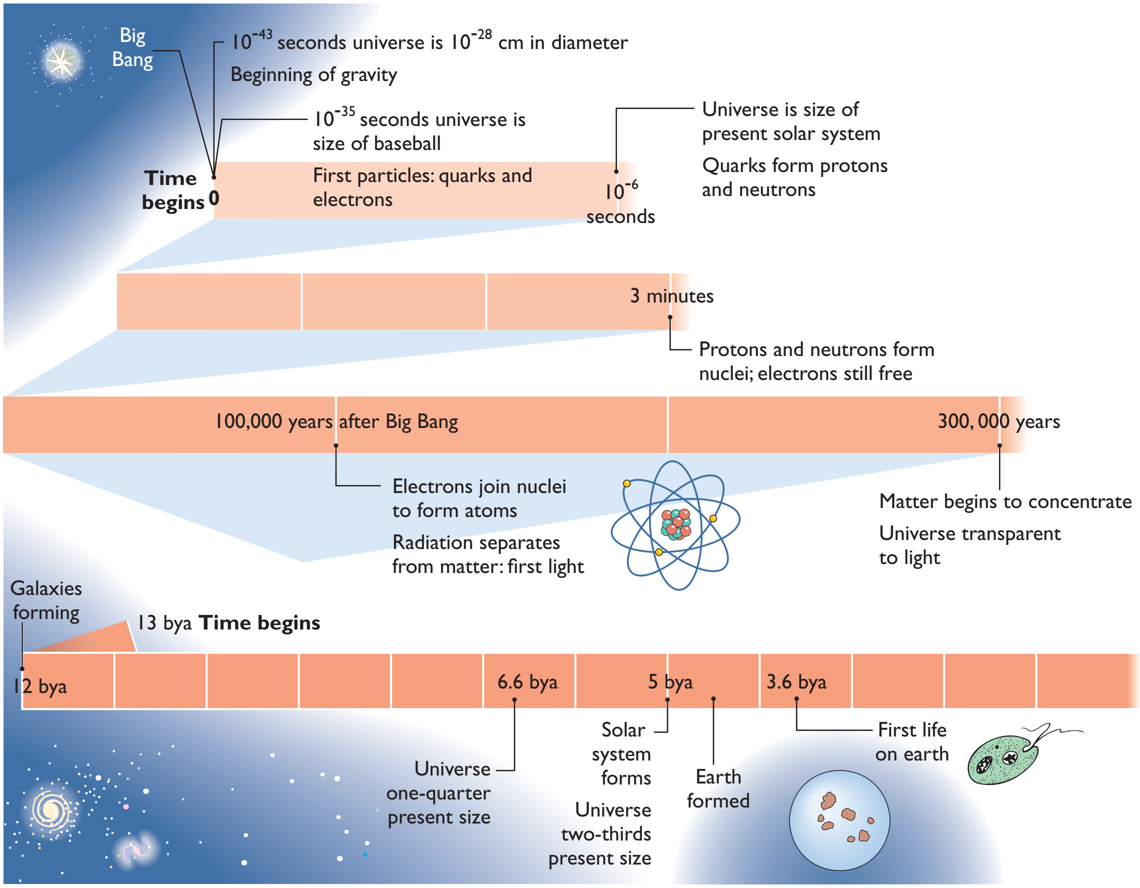

Big Bang
10^-43 seconds universe is 10^-28 cm in diameter
Beginning of gravity
10^-35 seconds universe is size of baseball
Universe is size of present solar system
Quarks form protons and neutrons
Time begins 0
First particles: quarks and electrons
10^-6 seconds
3 minutes
Protons and neutrons form nuclei; electrons still free
100,000 years after Big Bang
300, 000 years
Electrons join nuclei to form atoms
Radiation separates from matter: first light
Matter begins to concentrate
Universe transparent to light
Galaxies forming
13 bya Time begins
12 bya
6.6 bya
5 bya
3.6 bya
Universe one-quarter present size
Solar system forms
Universe two-thirds present size
Earth formed
First life on earth

FIGURE 6.1
History of the universe, from the Big Bang to the origin of life on earth. The scale of the timeline changes because some events are condensed into incredibly small periods and others are stretched over unimaginable spans.

amino acids, the building blocks of proteins. But as you recall, proteins cannot be built without a nucleic acid code. Evidence now suggests that RNA formed very early in earth's history. RNA was able to replicate itself and act as a code for the synthesis of proteins. Later, DNA took over this role (Orgel 1994). It is still, of course, a long way from

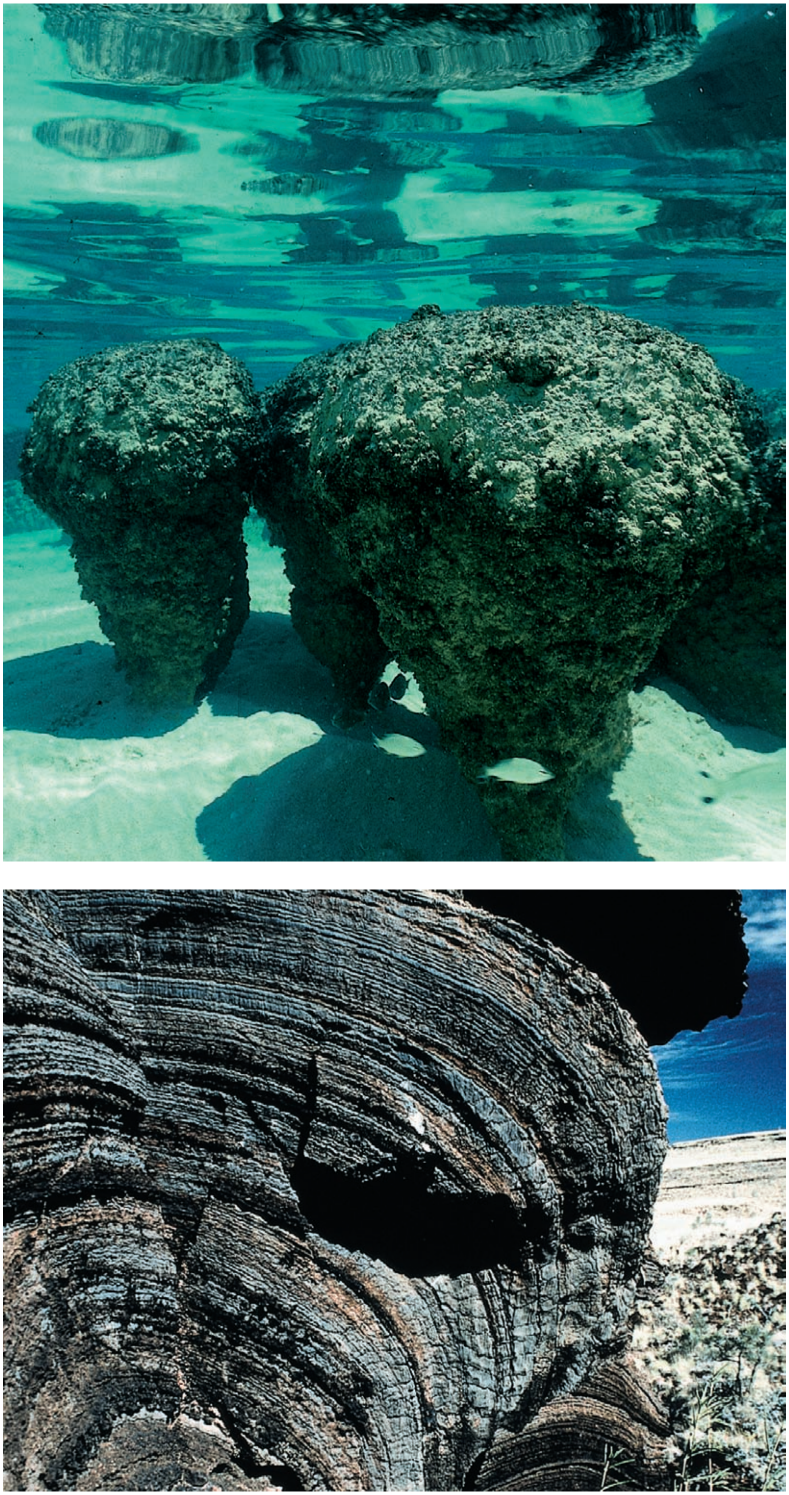


FIGURE 6.2
Stromatolites in Australia, (*top*) are formed when mats of blue-green algae (single-celled organisms) are covered with sand, silt, and mud, which the algae cement down and then grow over. Fossil stromatolites (*bottom*), and thus the organisms that made them, have been dated to 3.5 bya.

amino acids and RNA to a living organism, and the details of this path remain unclear.

Whatever happened, it happened fast (about 700 million years from the formation of the earth to life), but once established, life at first evolved slowly. The world's first identifiable organisms were simple single cells like bacteria (Figure 6.3). It wasn't until about 2 bya that complex single-celled organisms containing nuclei and organelles evolved (see Figure 3.1). Multicellular organisms first appeared about 1.7 bya. The earliest evidence for simple life on land—bacteria—dates to 1.2 bya.

All these early single-celled organisms reproduced **asexually** by splitting and making copies of themselves. Evolutionary change relied entirely on mutations. Then about 1 bya, some organisms began to reproduce **sexually.** Sexual reproduction may have begun as a mechanism of genetic exchange to replace defective genes. Soon, however, it proved to be an accelerator of evolution. Now, in addition to mutation, fertilization also provided genetic and phenotypic variation, and evolutionary change quickly gained speed. Figure 6.4 summarizes what is known about the timing of important events in the evolution of life on earth.

About 543 mya, in the Cambrian period, complex multicellular organisms burst on the scene. Some possessed hard parts like shells. So apparently sudden and rapid was this event that it is referred to as the *Cambrian* Explosion. In a mere 5 million years, all major body plans of multicellular animals had evolved, including ancestors of the **vertebrates,** animals with backbones (Figure 6.5). So far, there are no agreed-upon explanations for this "explosion," but it is clearly a major event in the history of life, and it set the themes for the subsequent evolution of animals.

By 470 mya, plants and fungi had colonized the land. Fish had evolved and land animals had appeared by 425 mya. Insects appeared about 400 mya; by 350 mya, some of them had evolved wings. Reptiles showed up around 350 mya as well, and the reptilian form that is thought to have given rise to the mammals was found at about 256 mya. Dinosaurs began evolving around 235 mya, with true mammals appearing about 220 mya. Sometime around 150 mya, feathers evolved by a group of dinosaurs signaled the beginning of the evolution of birds (see Figure 5.4). Flowering plants appeared only a little more than 100 mya, and the primates, the group to which humans belong, showed up at least 55 mya and probably earlier.

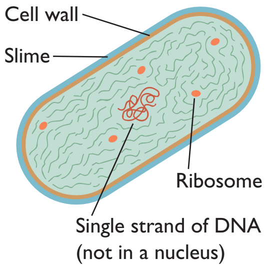


FIGURE 6.3
This typical bacterium represents some of the earliest forms of life on earth and what are still—in terms of time and numbers—the dominant forms of life today.

asexually Reproducing without sex, by fissioning or budding.

sexually Reproducing by combining genetic material from two individuals.

vertebrates Organisms with backbones and internal skeletons.

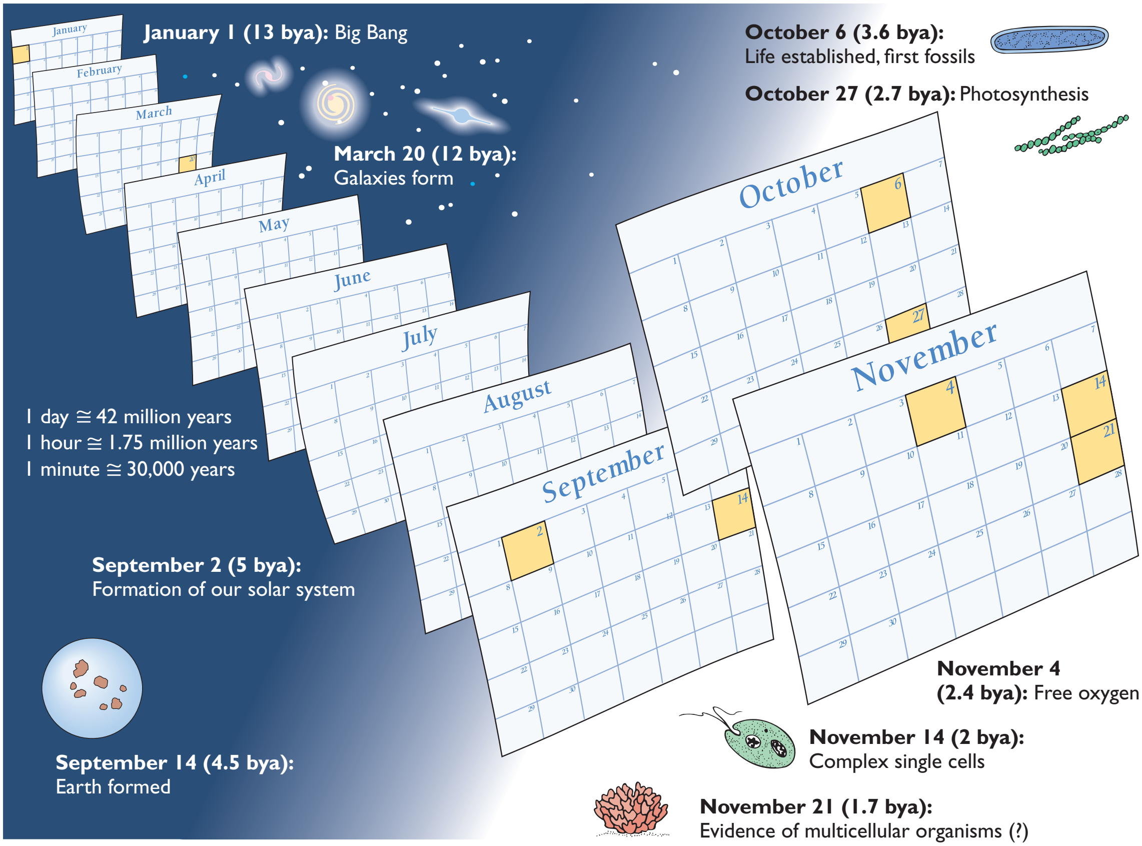

January
February
March
April
May
June
July
August
September
October
November
January 1 (13 bya): Big Bang
March 20 (12 bya): Galaxies form
1 day ≅ 42 million years
1 hour ≅ 1.75 million years
1 minute ≅ 30,000 years
September 2 (5 bya): Formation of our solar system
September 14 (4.5 bya): Earth formed
October 6 (3.6 bya): Life established, first fossils
October 27 (2.7 bya): Photosynthesis
November 4 (2.4 bya): Free oxygen
November 14 (2 bya): Complex single cells
November 21 (1.7 bya): Evidence of multicellular organisms (?)

FIGURE 6.4
Astronomer Carl Sagan likened the history of the universe to a single calendar year in his 1975 Pulitzer Prize–winning book, *The Dragons of Eden*. This calendar has been recalculated to show the currently accepted dates for important events.
(Adapted from Sagan, 1977)

plate tectonics The movement of the plates of the earth's crust, caused by their interaction with the molten rock of the earth's interior. The cause of continental drift.

DRIFTING CONTINENTS AND MASS EXTINCTIONS: THE PACE OF CHANGE

During all this time, life was not the only thing evolving on earth. The earth itself was also evolving as the continents changed shape and position, a phenomenon known as *continental drift*, which operates through the process of **plate tectonics.** The outer layer of rock on the earth, the *crust*, is in

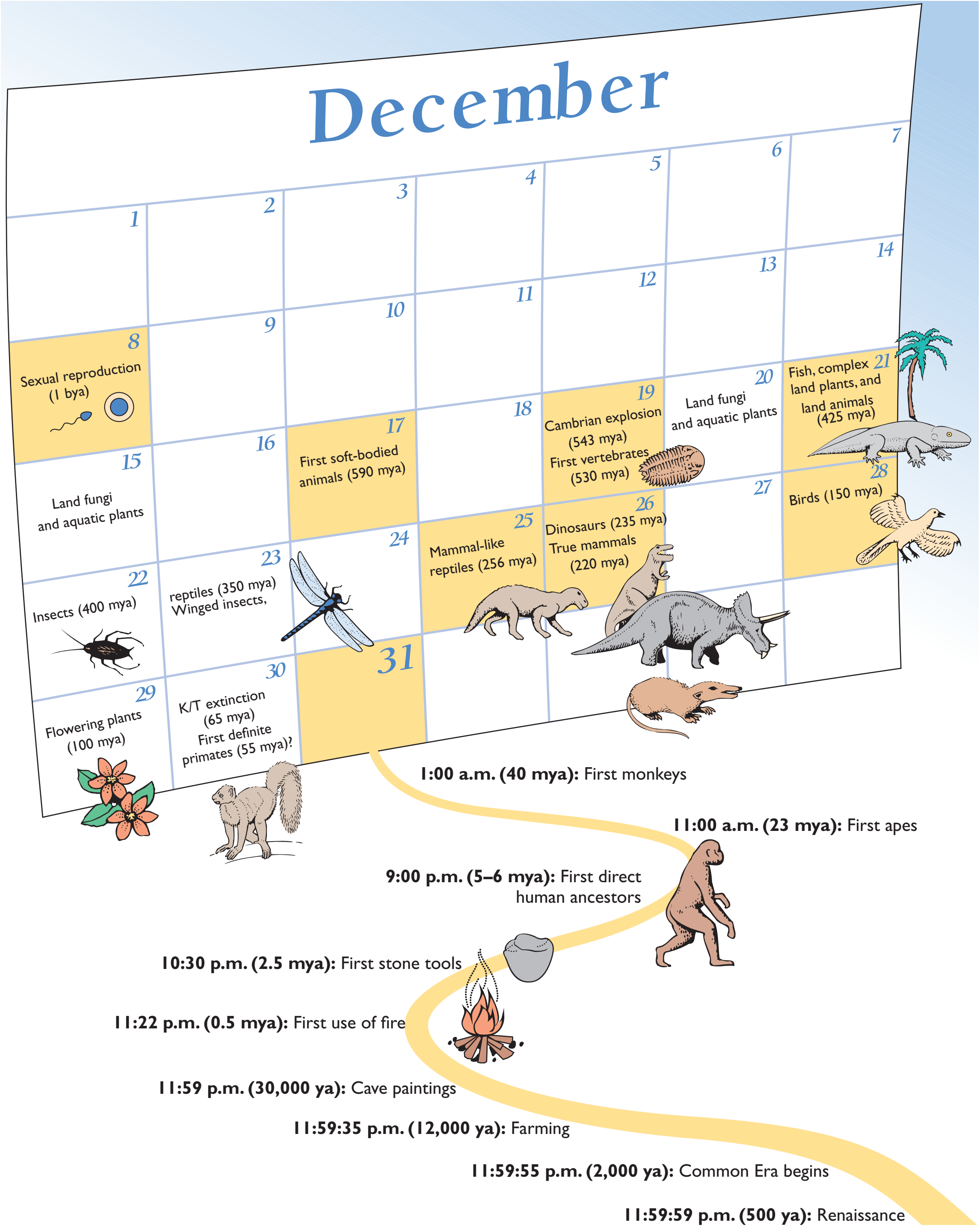

December
1
2
3
4
5
6
7
8
Sexual reproduction (1 bya)
9
10
11
12
13
14
15
Land fungi and aquatic plants
16
17
First soft-bodied animals (590 mya)
18
19
Cambrian explosion (543 mya)
First vertebrates (530 mya)
20
Land fungi and aquatic plants
21
Fish, complex land plants, and land animals (425 mya)
22
Insects (400 mya)
23
Winged insects, reptiles (350 mya)
24
25
Mammal-like reptiles (256 mya)
26
Dinosaurs (235 mya)
True mammals (220 mya)
27
28
Birds (150 mya)
29
Flowering plants (100 mya)
30
K/T extinction (65 mya)
First definite primates (55 mya)?
31
1:00 a.m. (40 mya): First monkeys
11:00 a.m. (23 mya): First apes
9:00 p.m. (5–6 mya): First direct human ancestors
10:30 p.m. (2.5 mya): First stone tools
11:22 p.m. (0.5 mya): First use of fire
11:59 p.m. (30,000 ya): Cave paintings
11:59:35 p.m. (12,000 ya): Farming
11:59:55 p.m. (2,000 ya): Common Era begins
11:59:59 p.m. (500 ya): Renaissance

FIGURE 6.4 (*Continued*)

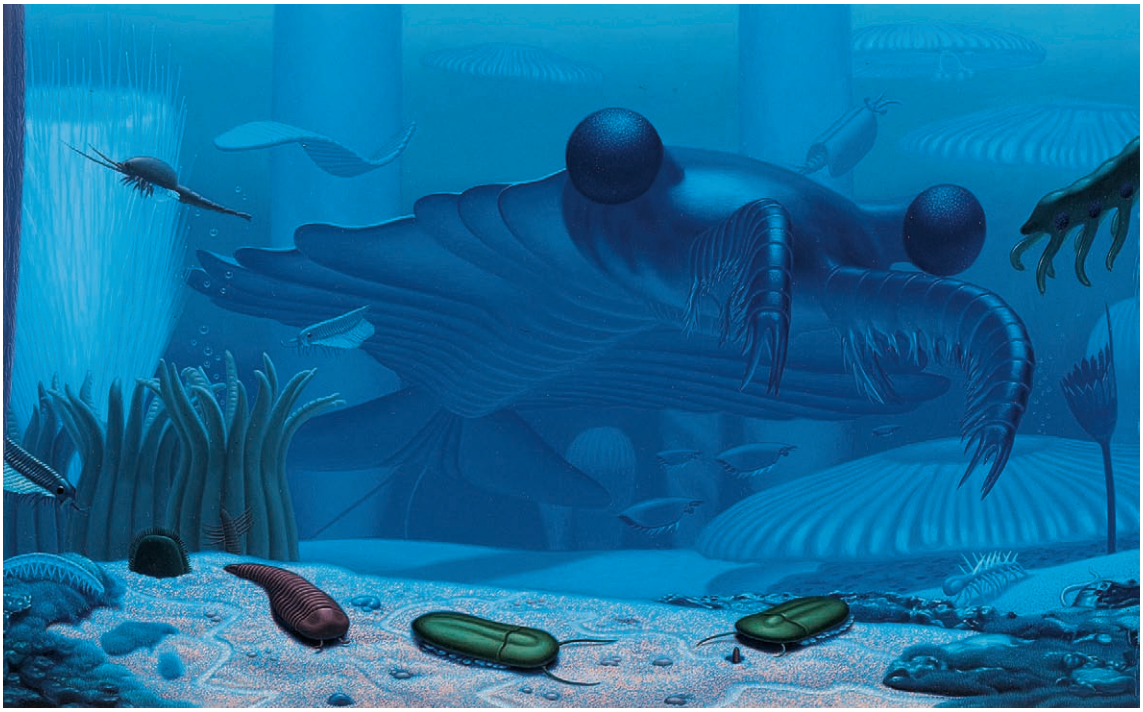
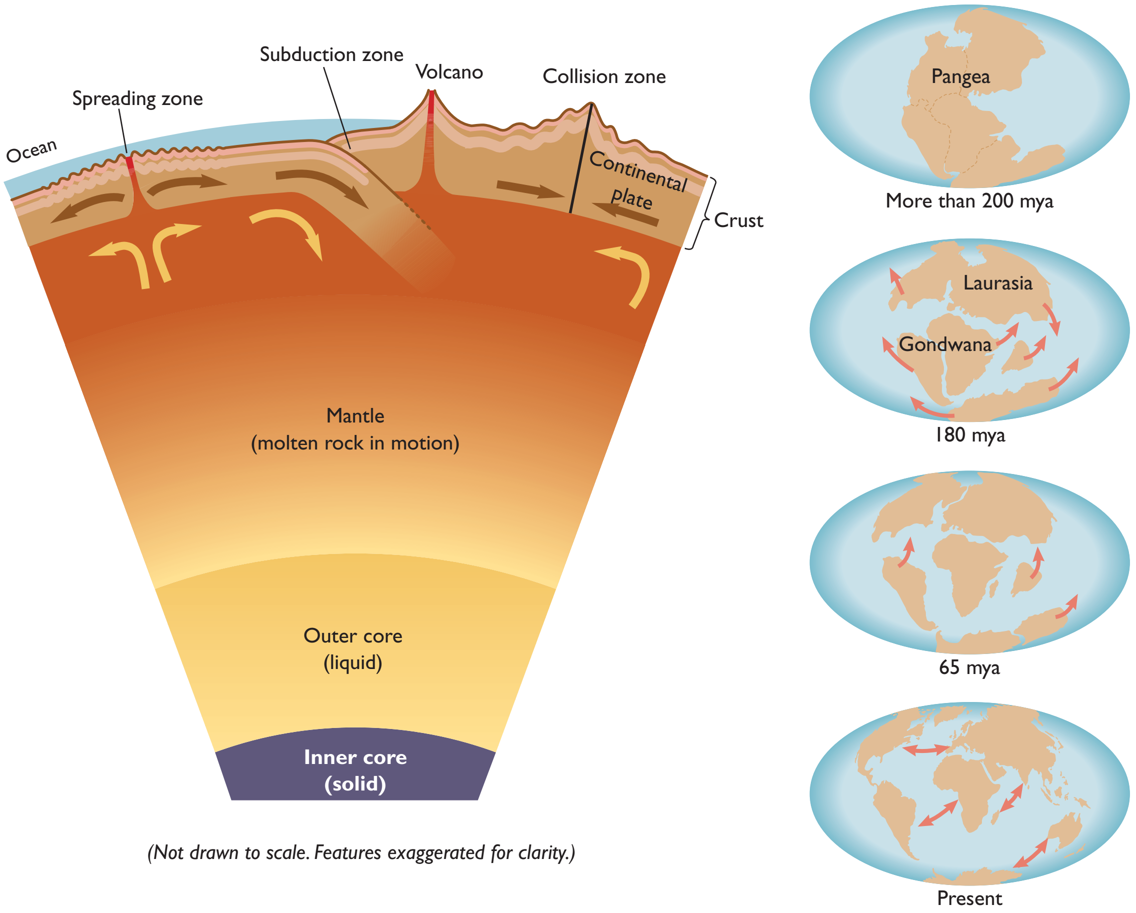


FIGURE 6.5
Cambrian fauna consisted mostly of arthropods, ancestors of modern-day insects, spiders, and crustaceans. The large creature in the center grew to 3 feet long.

a constant state of change. It is broken into some sixteen *plates* of various sizes that fit together like a huge spherical jigsaw puzzle. The motion of the molten rock, *magma,* below the crust causes the plates to change shape and location. In some areas, magma seeps up between the plates and solidifies, pushing the plates apart. Something has to give, and at other boundaries called *subduction zones*, one plate is pushed under another and plunges deep within the earth, where it melts and adds to the magma. Clearly, then, the continents—those parts of the plates that protrude above sea level—have shifted over time and will continue to do so (Figure 6.6). Plate tectonics accounts for important geological phenomena. Where the plates meet and move against one another, tremendous forces are produced that result in earthquakes and volcanoes and cause mountains to grow.

Pangea The supercontinent that included parts of all present-day landmasses.

By the time the dinosaurs and early mammals appeared, all the continents had drifted together to form a huge supercontinent we call **Pangea,** literally "all lands." This is why, for example, we find fossils of the same type of dinosaur in what are now such widely separated places as China, North America, and Antarctica. Around 200 mya, Pangea began to


Subduction zone
Volcano
Collision zone
Spreading zone
Ocean
Continental plate
Crust
Mantle
(molten rock in motion)
Outer core
(liquid)
Inner core
(solid)
Pangea
More than 200 mya
Laurasia
Gondwana
180 mya
65 mya
Present

(Not drawn to scale. Features exaggerated for clarity.)

FIGURE 6.6
This cross section of the earth shows the process of plate tectonics and the resultant drift of the continents over the past 200 million years. Continental drift, of course, occurred prior to 200 mya and will continue into the future.

break up, and the resulting landmasses—the ancestors of our present-day continents—drifted over the globe, producing a diversity of environments and geographic boundaries that has profoundly affected the nature of life on earth as we know it today.

From all we've discussed so far, it would seem that the evolution of the earth and of life—influenced by continental drift and the environmental changes it brings about—has been a steady process. And basically it has been—relative to the immense amount of time involved. But the fossil record shows that at least five times in the planet's history some change has taken place that was so rapid and extensive that it radically altered the course of biological evolution by causing a mass extinction.

For example, about the time the continents were drifting together to form the supercontinent of Pangea—250 mya—over 95 percent of

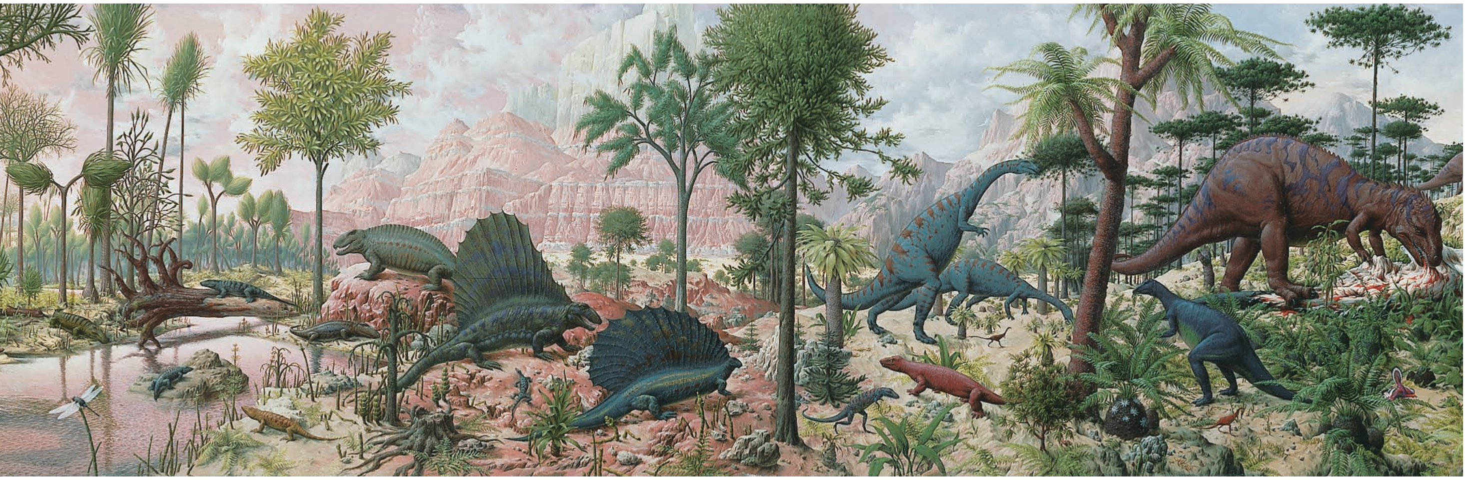


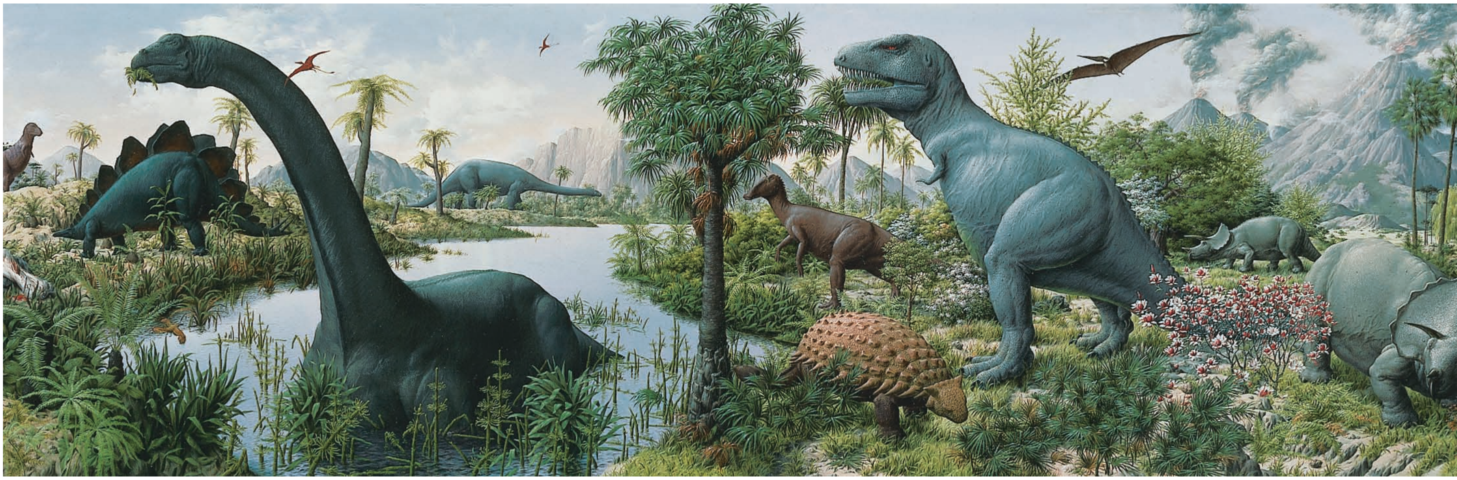
FIGURE 6.7
This painting, by Rudolph Zallinger, reflects some now outdated ideas about the appearance and behavior of the dinosaurs. It does show, however, some of the variety of these creatures as they existed over 170 million years of time (*from left to right in the mural*). The dinosaurs once dominated the earth's environments.

all species of marine and terrestrial organisms suddenly became extinct. Some changes occurred to which none of the variants within all those species were adapted. The cause for this greatest of all mass extinctions is still debated, but a new hypothesis suggests it was the result of massive volcanic eruptions, possibly initiated by a meteor impact in what is now Siberia, that altered the planet's climate. At any rate, such a catastrophe certainly had a major effect on the future course of life's evolution.

Another mass extinction directly affected the evolution of our small section of the evolutionary tree. About 65 mya, the dinosaurs were a dominant form of land animals. There were large reptiles in the seas and close relatives of the dinosaurs in the air (Figure 6.7). Mammals were also around and had been for nearly as long as the dinosaurs and had already begun to diversify into some of the forms known today.

Then one day—literally—an asteroid, thought to measure 6 miles across, crashed through the earth's atmosphere and into the crust where the north coast of the Mexican Yucatán is now. The impact made a crater 200 miles in diameter. The asteroid may have broken apart on impact with the atmosphere, and pieces may have hit in other locations as well.

This collision created a blast like that of a nuclear explosion. Thousands of cubic miles of vaporized rock, water vapor, and small particles and dust were shot into the atmosphere and carried around the world. Heat from the impact caused massive forest fires that created smoke and



ash. One hypothesis suggests that the impact produced shock waves that bounced inside the earth and were focused on the opposite side of the planet, causing large-scale volcanic activity in what is now India, which put even more smoke and ash into the air. It has been noted that the Yucatán is rich in sulfur, suggesting that the impact might have produced sulfuric acid in the atmosphere, causing acid rain. All this matter created a blanket that blocked sunlight, cooling the earth and preventing green plants from carrying out photosynthesis.

These extensive environmental changes proved disastrous (a word that means, appropriately, "bad star"). Dinosaurs became extinct, along with every other species of land animal weighing more than about 55 pounds, many plants, and much of the ocean's plankton, the small organisms that provide a great deal of the world's oxygen and that serve a vital role at the base of the food chain. This event is the famous *Cretaceous/Tertiary (K/T) extinction*.

But many of the mammals survived. By a stroke of luck, they were already adapted to withstand adverse, changing conditions. Now, with the dinosaurs suddenly gone, a whole world of niches was opened to them and to many other creatures that had made it through the catastrophe. This group included some of the birds, the dinosaurs' only living direct descendants (Figure 6.8).

It took a while, but by about 40 mya, all the major types of mammals we know today had appeared—everything from bats to whales to a group

Contemporary Reflections

Are Mass Extinctions a Thing of the Past?

Extinction is part of evolution. For one reason or another, species become extinct all the time. An estimated 90 percent of all species that have ever existed are now extinct.

But the idea of some intense event that can bring about the extinction of up to 95 percent of the earth's living forms over a short period of time seems inconceivable to us. And yet, at least five such events have occurred over the 3.6-billion-year history of life on this planet. The best known of these wiped out the dinosaurs—a long-lived and very successful group of species—65 mya. Surely, we think, these events were part of the earth's "formative" years and could not happen again. Sadly, this view is incorrect—for two reasons.

First, we know that the mass extinction that included the dinosaurs was initiated by the impact of a huge asteroid, and impacts are associated with some of the other mass extinctions as well. Although such impacts were more common in the past, asteroids, comets, and fragments of them are far from used up. Lots of them still orbit through our solar system. Go outside on any clear night, look up long enough, and you're bound to see one of the smaller ones burn up as it hits the earth's atmosphere. These are so-called shooting stars. Bigger ones, parts of which survive the atmosphere, hit the earth regularly (although most are neither seen nor found).

And on occasion we encounter very large ones. A few years ago, an asteroid large enough to do serious damage missed the earth by a mere 250,000 miles—the distance between the earth and the moon, a near miss on the cosmic scale. It was not seen until it had already passed us!

In 1908 a large portion of an asteroid or a fragment of a comet nucleus exploded 6 miles up in the atmosphere over Siberia. The shock waves were heard 600 miles away and flattened trees over 770 square miles. It's altogether possible, then, that our planet will be hit by another large object from space in the future, and if it's big enough, devastating consequences will follow, including the extinction of many species.

But there is a second reason why mass extinctions are not things of the past—a reason even more disturbing since (unlike the situation with asteroids) we *could* do something about it. There is, in fact, a sixth mass extinction in earth's history, and it is happening right now.

Starting about 10,000 ya, species began becoming extinct at a rate faster than usual. At present, species are disappearing at a rate at least as fast as, and probably faster than, during any of the previous five mass extinctions. Estimates vary, but the earth may be losing species at a rate of 27,000 a year—that's 3 every hour. Now, one might argue that given what we know of earth's history, extinctions—even mass ones—are "natural." Well, they have been; but this one is different. Unlike the other extinctions, where the conditions causing the problem eventually went away, this situation is unlikely to get better because, as biologist Niles Eldredge says, "the irritant . . . remains on the scene" (1995:128). That "irritant," of course, is us.

Since we figured out how to control natural food sources through farming and animal husbandry some 12,000 ya, our species' population has grown at an ever-increasing rate. Our need for resources, energy, and space has grown along with our numbers. We have pushed other species into marginal areas, destroyed their habitats and resources, and hunted or otherwise exploited them to extinction. We are well into the process of changing the very climate of the earth as our emissions into the atmosphere are causing the world's climate to change.

Although we may or may not experience the catastrophic death and destruction of an asteroid impact, we are—*right now*—in the midst of what may be the biggest and fastest of all mass extinctions. Decidedly *not* a thing of the past.

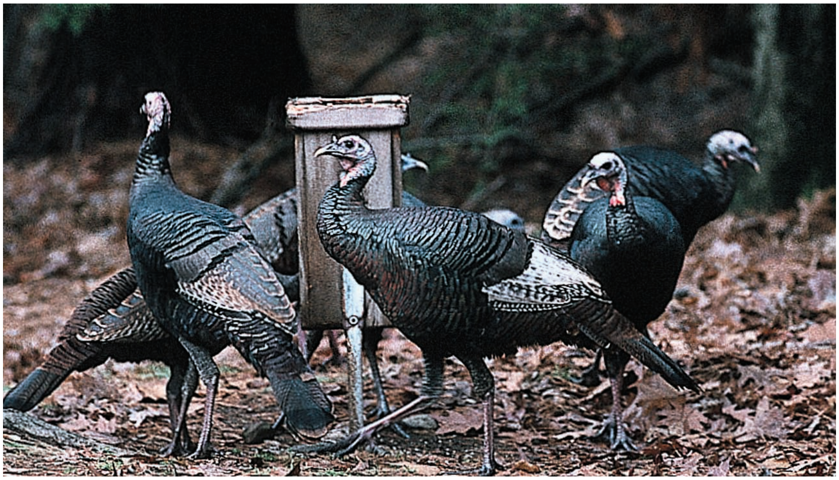


FIGURE 6.8 The wild turkey shows a striking similarity to bipedal dinosaurs, further evidence of the evolutionary relationship between dinosaurs and birds.

of tree-dwelling creatures possessed of acute eyesight, dexterous hands, and large, inquisitive brains. These were the primates, and it is this group that we shall focus on in the next chapters.

SUMMARY

This narrative of the history of the universe has been necessarily brief, but it does point out three themes that are important to remember as we continue.

First, it could be said—by virtue of human numbers (over 7 billion) and our impact on the planet—that we are the dominant species on the earth today. But our evolutionary history makes up a small fraction of the whole history of the universe and even of the earth. We are the new kids on the evolutionary block, and we have not as yet even proved ourselves successful by the criterion of longevity. Cockroaches have been around hundreds of times longer than we have; bacteria have been around since the beginning of the fossil record. By these standards, our species is in its infancy.

Second, as the Bible says, “there is no new thing under the sun.” Indeed, although we often speak of the “origin of the earth” or the “origin of life,” the only *real* origin is that of the universe itself. All the events subsequent to that have been *rearrangements* of what already existed: matter condensing from energy as it cools; large atomic particles forming from smaller ones; stars coming together from cosmic dust; heavy elements being created from lighter ones in the nuclear furnaces of those stars; the elements of inorganic molecules being rearranged to form the molecules of life; and the shuffling of the genetic code, producing the extraordinary multitude of living things that have inhabited this planet.

Third, and perhaps most humbling, the specific history of the universe, including the earth and its life, could have happened in countless other ways. Each event in our story is contingent on preceding events. Even our evolution is dependent on the specific sequence of events that came before it. If those events had been different, *we* might be different—or we might not be here at all. Imagine if that asteroid had *not* hit the earth 65 mya. In other words, the evolution of humans—or anything else for that matter—was not inevitable. We're lucky we're here.

QUESTIONS FOR FURTHER THOUGHT

1. Consider a question from Chapter 5 from a more specific perspective: We humans may be bringing about the extinction of a large number of other species, but for some of them, what real difference does it make? We hear about such endangered species as the snail darter (a small North American fish), the spotted owl, and the Texas blind salamander. Would it really matter, beyond an ethical or an aesthetic consideration, if any of these became extinct?
2. The astronomer Carl Sagan once referred to human beings as "star stuff." He meant it literally. How so? What does this say about the nature of evolution, both on a biological and a cosmic level?

KEY TERMS

photosynthesis
organic
inorganic
asexually
sexually
vertebrates
plate tectonics
Pangea

SUGGESTED READINGS

Many of these suggested readings are a few years old, but they are still accurate and well-done. If anything, the situation with extinctions has worsened.

For a good summary of cosmology—the history of the universe—see the February 2000 issue of *Natural History*, especially "Genesis: The

Sequel," by Alan Guth. For a good discussion of the science behind our understanding of the history of the universe, I recommend *Coming of Age in the Milky Way*, by Timothy Ferris.

The evolution of life is covered in the lavishly illustrated *The Book of Life*, edited by Stephen Jay Gould. For a good narrative approach, see *Life*, by Richard Fortey, and for a more technical but still readable work, see *History of Life*, second edition, by Richard Cowen. *National Geographic* has a series of articles called "The Rise of Life on Earth" in the March 1998, April 1998, May 1999, February 2000, and September 2000 issues.

The Cambrian explosion is the subject of an article by R. Gore in the October 1993 *National Geographic:* "The Cambrian Period: Explosion of Life." It is also the focus of Stephen Jay Gould's *Wonderful Life* and Simon Conway Morris's *The Crucible of Creation*. These two well-respected authorities disagree on the meaning of the Cambrian fossils and the nature of evolution as a series of contingent events. For a summary of their debate, see "Showdown on the Burgess Shale," by Conway Morris and Gould, in the December 1998/January 1999 *Natural History*.

For a good discussion of the origin of feathers, see "Which Came First, the Feather or the Bird?" by Richard O. Prum and Alan H. Brush in the March 2003 *Scientific American*. And for some of the newest evidence of the dinosaur-bird link, see "Feather Quill Knobs in the Dinosaur *Velociraptor*," by Alan Turner, Peter Makovicky, and Mark Norell in the 21 September 2007 *Science*.

An article on those volcanoes in India, with some impressive pictures, is in the 21 March 2008 *Science*, in "Sulfur and Chlorine in Late Cretaceous Deccan Magmas and Eruptive Gas Release," by Stephen Self et al. Don't let the title put you off; look at the pictures.

New research on the evolution of mammals is in "Transformation and Diversification in Early Mammal Evolution," by Zhe-Xi Luo in the 13 December 2007 *Nature*.

The subject of mass extinctions in general is discussed in Edward O. Wilson's *Diversity of Life* and in an article in the June 1989 *National Geographic:* "Extinctions," by R. Gore.

The link between extraterrestrial collisions and mass extinctions is explored in "Repeated Blows," by Luann Becker, in the March 2002 *Scientific American*.

To see animations of continental drift, go to www.scotese.com/pangeanim.htm. A good site on the geology of North America is http://tapestry.usgs.gov/Default.html. It's called "A Tapestry of Time and Terrain" and features a section called "Rocks of Ages" that discusses the different geological divisions of earth history.

CHAPTER 7

The Primates

I confess freely to you, I could never
look long upon a monkey, without
very mortifying reflections.
—William Congreve (1695)

"The proper study of mankind is man," said the poet Alexander Pope. The last few chapters should have convinced you that even biological anthropologists, who by definition focus on the study of humankind, cannot limit their interests to just our own species. The processes that have produced modern *Homo sapiens* are the processes that have produced every single species that has ever inhabited this planet. All those species are part of an integrated whole, composed of all environments and all living things in complex interaction with one another across geographical space and through evolutionary time.

Were we to limit our study just to our species, we would lose a great deal of perspective. We need to compare ourselves with other forms of life to see in what ways we are similar and in what ways we differ. This comparison is made all the more important because we *are* the species we are studying, and so it can be difficult to be objective about ourselves. Thus, primatology is an important part of anthropology.

In this chapter we will address several important questions:

What is our place in nature; where do we fit—from a scientifically objective point of view—in the world of living things?

What are the characteristics of the primates—the group of animals of which we are a part?

In what ways are humans like the other primates? In what ways are we unique?

How should we classify ourselves?

NAMING THE ANIMALS

Recognition of some relationship among living things is not new. It is probably as old as human intellect itself. But formalizing this recognition was not always seen as important, even to the emerging science of biology at the beginning of the eighteenth century. After all, plants and animals were then thought to be the unchanging products of divine creation, and an understanding of the evolutionary implications of biological relationships was many years in the future.

One eighteenth-century biologist, however, thought that a formalized view of the relationships was important, even though he thought species were specially created and forever fixed. This was the Swedish botanist Carl von Linné (1707–1778), introduced in Chapter 2, known to us by his Latinized name, Carolus Linnaeus. Linnaeus sought to devise a system of names that would reflect the relationships among all the plants and animals on earth. He felt, of course, that he was proposing a way to describe what God had in mind when He created living things. The system he came up with is still used today, and it carries more meaning than Linnaeus dreamed it would.

Linnaeus created a system of nested categories of increasing specificity, a hierarchical arrangement in other words. The largest category contains gradually smaller categories, ending with the most specific, the species. Such a classification system is known as a **taxonomy,** and Linnaeus proposed his taxonomy for living organisms in his *Systema Naturae*, published in final form in 1758.

Our present taxonomic system, based on Linnaeus's original scheme, uses seven (or more when needed) basic categories: kingdom, phylum (plural, *phyla*), class, order, family, genus (plural, *genera*), and species. Each organism classified is given a name indicating its place within each of these categories and, thus, its relationship to other organisms. Table 7.1 shows a taxonomy of five familiar species.

All these are obviously members of the animal kingdom and share inclusion in phylum Chordata (essentially, animals with internal skeletons, especially backbones) (Table 7.2). All are also obviously mammals, and all are primates (the group we'll describe in detail later). But then, as you can see at a glance, they divide into two intuitive groups: one group comprises humans; the other is made up of the apes, which all share some common phenotypic features. Thus, they separate at the family level. The chimp and bonobo share a genus but differentiate at the species level. So, even if you didn't know these animals, you could tell how they are related, phenotypically, to one another.

taxonomy A classification using nested sets of categories of increasing specificity.

TABLE 7.1
Traditional Linnaean Taxonomy of Five Familiar Species

	Human	*Chimpanzee*	*Bonobo*	*Gorilla*	*Orangutan*
Kingdom	Animalia	Animalia	Animalia	Animalia	Animalia
Phylum	Chordata	Chordata	Chordata	Chordata	Chordata
Class	Mammalia	Mammalia	Mammalia	Mammalia	Mammalia
Order	Primates	Primates	Primates	Primates	Primates
Family	Hominidae	Pongidae	Pongidae	Pongidae	Pongidae
Genus	*Homo*	*Pan*	*Pan*	*Gorilla*	*Pongo*
Species	*sapiens*	*troglodytes*	*paniscus*	*gorilla*	*pygmaeus*

As far as Linnaeus knew, he was describing a static, divinely created system of living things. We now know that a taxonomy also reflects evolutionary relationships, because the degree of similarity between two organisms is a direct result of the amount of time they have been evolutionarily separated. So, although a taxonomy can't tell us specific dates for branchings, we can infer from it the relative times of these evolutionary events.

Figure 7.1 is a tree showing the relative times of branching for the five primates in the table, inferred from their taxonomic categories. Each taxonomic difference is reflected by a branching point on the tree.

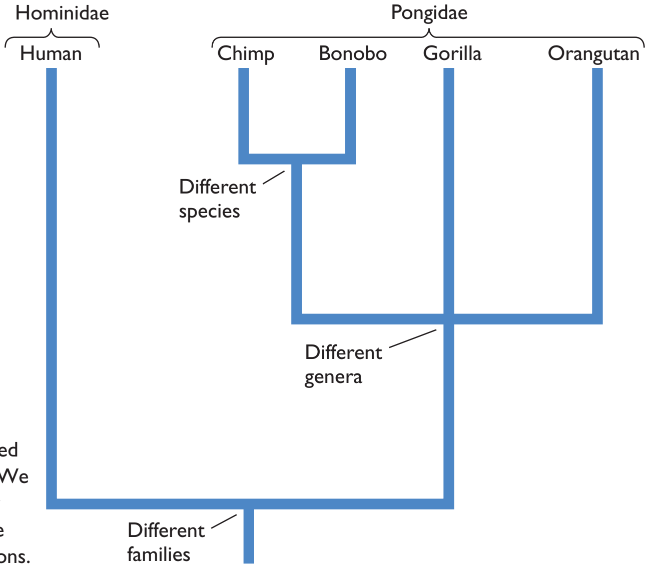


FIGURE 7.1
Evolutionary tree based on phenetic analysis. We infer the evolutionary relationships from the taxonomic classifications.

TABLE 7.2
Traditional Linnaean Taxonomy of Humans (with defining criteria)

Kingdom	***Animalia***	Ingestion Movement Sense organs
Phylum	***Chordata***	Notochord (includes Vertebrates)
Class	***Mammalia***	Hair Warm-blooded Live birth Mammary glands Active and intelligent
Order	***Primates***	Arboreal Developed vision Grasping hands Large brains
Family	***Hominidae***	Habitual bipeds
Genus	***Homo***	Toolmaking Omnivore
Species	***sapiens***	Brain size 1,000–2,000 ml*

**Note:* This definition is a matter of controversy and will be taken up in Chapter 11.

phenetic A classification system based on existing phenotypic features and adaptations.

cladistic A classification system based on order of branching rather than on present similarities and differences.

These are the basics of biological taxonomy, of the method called **phenetic**. There is, however, another way of classifying organisms. It, in a sense, works the opposite of Linnaeus's system because instead of inferring an evolutionary tree from a phenotypic classification, it establishes the actual pattern of branching of related organisms and then names the various groups that the resulting tree indicates. This is called **cladistic**. The debate over which method is better to meet the scientific goal of accurately describing nature is complex and beyond the scope of this book. But one aspect of the debate is relevant to anthropology, and we will take it up after we have described and surveyed the primates, the large and distinct order of which we are a part.

WHAT IS A PRIMATE?

There are an estimated 200 to 300 living species of primates. We're not sure how many have existed during the order's evolutionary history of more than 55 million years. Primates range from the very small, such as the mouse lemur of Madagascar, which weighs less than 3 ounces, to the gigantic—*Gigantopithecus*, an extinct ape from China, Vietnam, and India that may have stood 12 feet tall and weighed over half a ton (Figure 7.2).

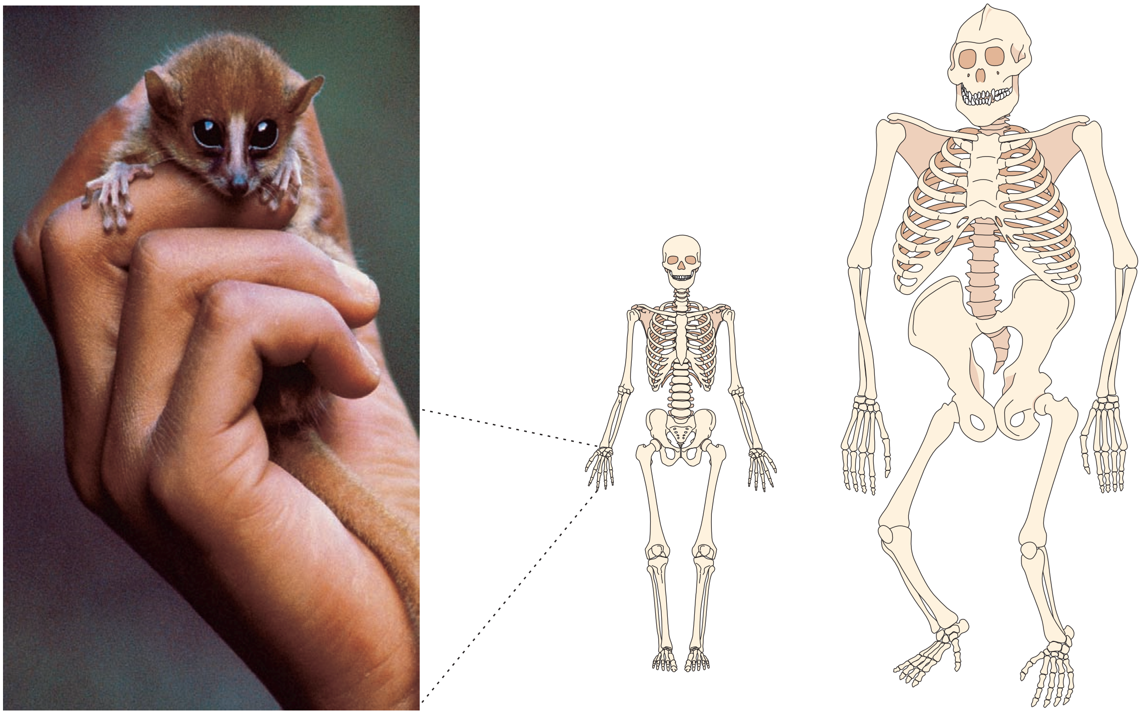


FIGURE 7.2
Here we compare a mouse lemur, the smallest living primate, with a human and with *Gigantopithecus,* now extinct, the largest primate ever (see Chapter 10).

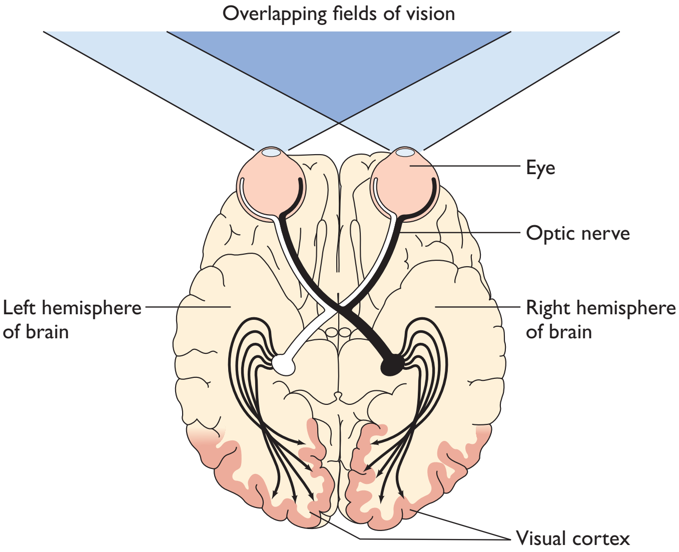


FIGURE 7.3
Stereoscopic vision. The fields of vision overlap, the eyes see the same view from different angles, and the optic nerve from each eye travels to both hemispheres of the brain. The result is true depth perception.

Some primates inhabit small, very specific environmental ranges and spend their lives slowly moving through the trees, eating fruits, leaves, or insects; one species of primate lives in nearly every environment and produces its own food.

Its wide variety makes the primate order a bit difficult to define in a simple sentence. The primates are best defined by looking at the characteristics they have in common and in seeing how these traits facilitate the primate adaptive strategy. We'll look at the primate traits by using the following categories: (1) the senses, (2) movement, (3) reproduction, (4) intelligence, and (5) behavior patterns.

The Senses

Bats and dolphins live in worlds of sound. Dogs live in a world of smells. The primates live in a visual world. Vision is the primates' predominant sense.

About 60 percent of the primates see in color, and all primates see in three dimensions. They have true depth perception (technically called **stereoscopic vision**), which is possible because of their anatomy and neurology (Figure 7.3). The nerves and muscles of most primate eyes are enclosed within a protective bony socket. Look at your surroundings. What you are able to see is what the majority of primates could see if they were in your place.

stereoscopic vision
Three-dimensional vision; depth perception.

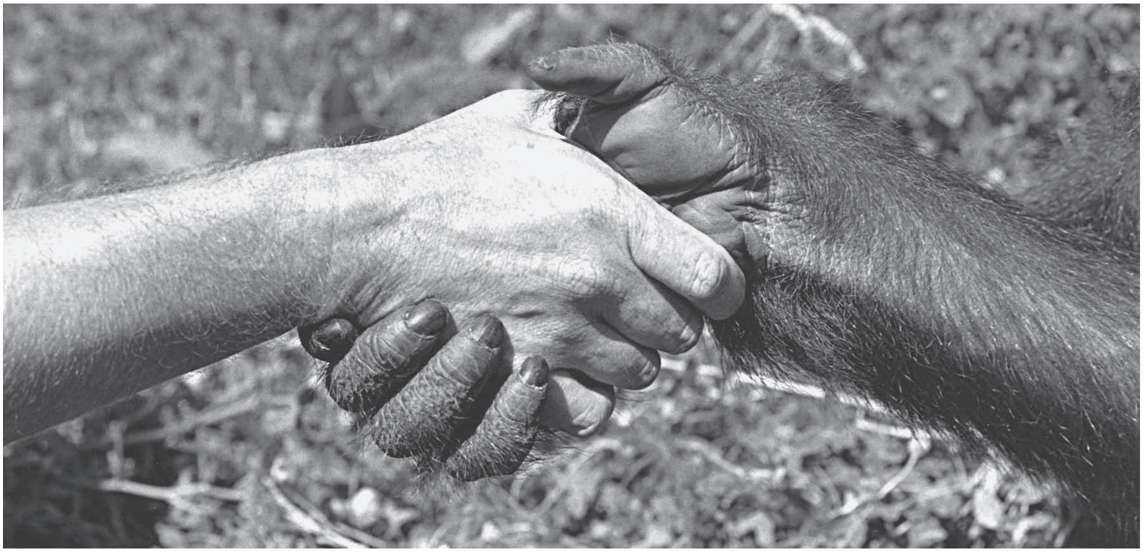


FIGURE 7.4
An orangutan holding its trainer's hand demonstrates the prehensile grip shared by nonhuman and human primates.

Other primate senses are not as acute as in many mammals. Primates lack the auditory (hearing) and olfactory (smelling) sensitivity of such familiar animals as dogs, cats, and cattle. Furthermore, and obviously related to the less acute sense of smell, primates tend to lack a snout and so have a relatively flat face. There is, as you might expect for a group of hundreds of species, some variation among primates. Many members of one group of primates (the prosimians, which we'll discuss later in this chapter) are nocturnal and lack color vision, but they have better senses of smell and hearing than do monkeys, apes, and humans.

Movement

Like most mammals, primates are, with one exception, **quadrupedal.** Although many primates can stand or even walk on two legs for short periods, humans are the only habitually **bipedal** primates. Unlike most mammals, primates have extremely flexible limbs, and their hands (and in most cases their feet) have the ability to grasp objects; that is, they are **prehensile** (Figure 7.4). Primates use this trait for several forms of locomotion. Some primates, called *vertical clingers and leapers*, jump from branch to branch or trunk to trunk using the grasping ability of all four limbs (see Figure 7.11). The apes are *suspensory climbers*, with the ability to hang and climb by the arms (see Figure 7.15). An extreme form of this mode

quadrupedal	Walking on all four limbs.
bipedal	Walking on two legs.
prehensile	Having the ability to grasp.

of movement is **brachiation,** swinging arm-over-arm through the trees. When on the ground, most primates use all fours. Asia's orangutans walk on their fists. The African apes have a unique quadrupedalism, supporting themselves on the knuckles of their hands instead of the palms. Primate species may use one or more of these locomotor methods, depending on their anatomy and the situation.

In addition, most primates are able to touch their thumbs to the tips of the other fingers on the same hand, allowing them to pick up and manipulate small objects. This capacity is called **opposability.** Finally, most primates have nails rather than claws on the tips of the fingers and toes. These provide support for the sensitive tactile sense receptors of the fingers. In short, primates have manual dexterity. Some have a great degree of dexterity in the feet as well (see Figure 7.11).

Reproduction

Most primate species give birth to one offspring at a time. Several primates, such as some of the marmosets from South America and some of the lemurs from Madagascar, normally produce twins or triplets. As is typical of mammals, primate parents take an active role in the protection, nurturing, and socialization of their young. Mostly because of their large, complex brains and because of the importance of learning, young primates are dependent on adults and take a long time to mature. How long, of course, varies according to the size of the primate species. The primates, relative to size, have the longest period of **postnatal dependency** of any mammal.

Intelligence

Intelligence can be defined as the relative ability of an organism's brain to acquire, store, retrieve, and process information. These abilities are related to brain size and brain complexity. A bigger brain has more room for all the complex nerve connections that make it work, just as a very sophisticated computer must necessarily be larger than a simple one. (Brain size variation *within* a species is another matter; in humans, for example, no substantiated correlation has been shown between brain size, within the normal range, and any reasonable measure of intelligence.) But brain size must also be looked at in a relative way: How big is the brain compared to the body it runs? A sperm whale, with its 20-pound brain, has a brain ten times the size of the average human's. A sperm whale's body, however, is

brachiation Locomotion by swinging arm-over-arm.

opposability The ability to touch the thumb to the tips of the other fingers on the same hand.

postnatal dependency The period after birth during which offspring require the care of adults to survive.

intelligence The relative ability of the brain to acquire, store, retrieve, and process information.

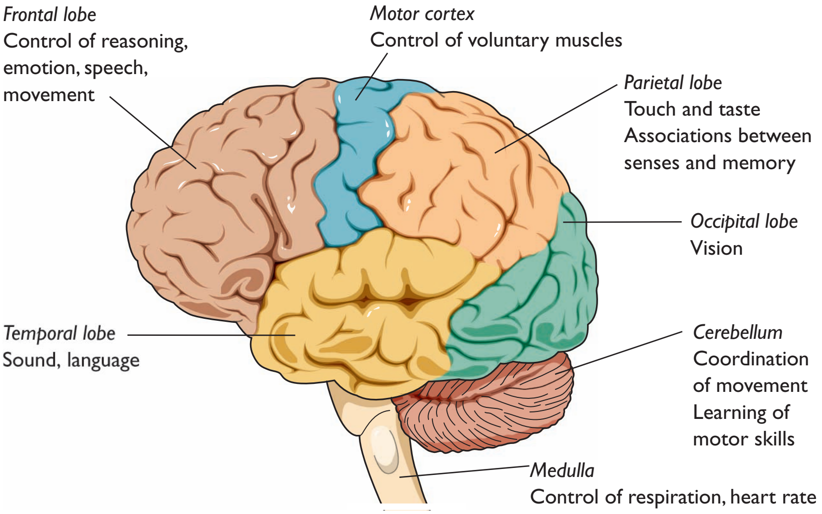

Frontal lobe
Control of reasoning, emotion, speech, movement
Motor cortex
Control of voluntary muscles
Parietal lobe
Touch and taste
Associations between senses and memory
Occipital lobe
Vision
Temporal lobe
Sound, language
Cerebellum
Coordination of movement
Learning of motor skills
Medulla
Control of respiration, heart rate

FIGURE 7.5
The human brain and its major parts and functions. The lobes and the motor cortex are all part of the neocortex.

over *five hundred* times the size of ours. We have bigger brains than whales have *relative* to the size of our bodies and this is true of the primates in general. Of all land mammals, the primates have the largest relative brain sizes. The human brain, however, is three times the size one would expect for a primate of our body weight.

In addition, the primate brain is complex, especially in the neocortex, that part of the brain where memory, abstract thought, problem solving, and attentiveness take place (Figure 7.5). In short, the primates are smart.

Behavior Patterns

Primates are social animals. Most primate species live in groups. Many other animals do too, but even those few primate species—such as orangutans—that usually remain solitary still interact with other members of their species in far more complex ways than, say, antelopes interact within a herd, or even wolves within a pack. The difference is that primates recognize individuals, and the individual primate holds a particular status relative to others in its group and to the group as a whole. A primate group is made up of the collective relationships among all its individual members. We will see these relationships in action when we examine primate behavior more closely in Chapter 8.

As physical evidence of the importance of these relationships, it may be noted that primates are among the most colorful of mammals, and most of the color patterns of many primates are displayed on their faces (Figure 7.6). The attention of one primate to another is drawn to the face, the primate's identity as an individual.

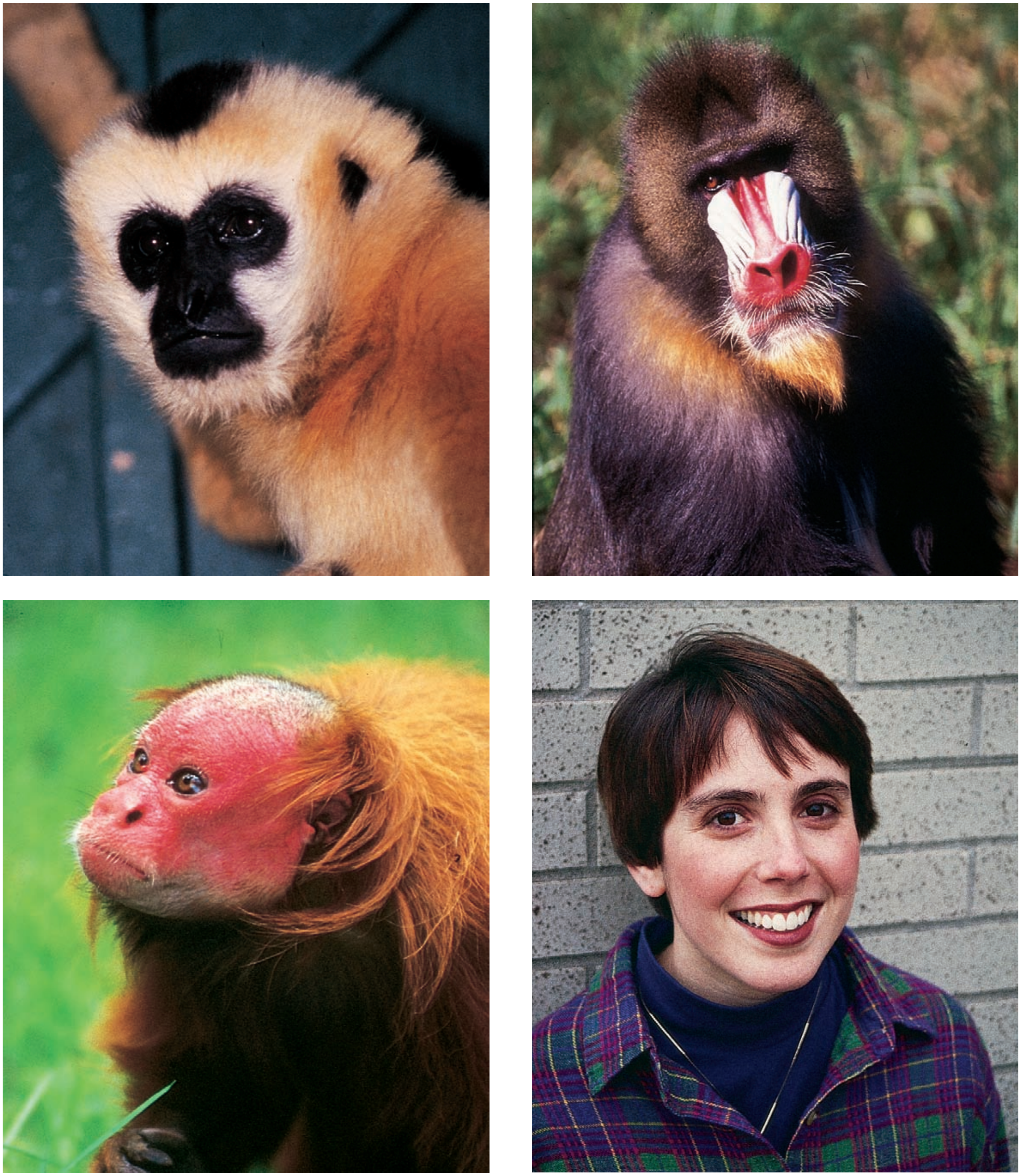


FIGURE 7.6
We see here some colorful primate faces, including that of one primate that purposely enhances the color. Colorful faces are evidence of the importance of individual recognition within primate societies. Shown here (*clockwise from upper left*) are a Chinese white-handed gibbon, a mandrill, a human, and a bald uakari.

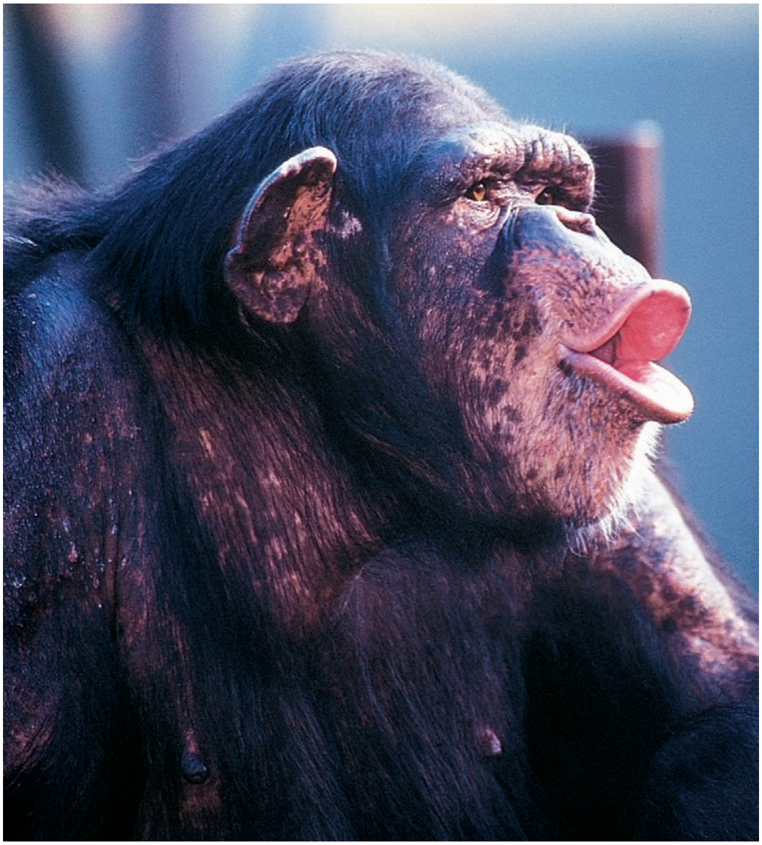
FIGURE 7.7
Male baboon protecting mother and young. The female holding her baby at left was being threatened by the boisterous play of a group of adolescent males, out of the picture to the right. The adult male in the center stepped in and barked at the group, which quickly took its play elsewhere. (These baboons are part of a captive troop.)

In some primates—baboons and chimpanzees, for example—each individual may have a rather specific status within the group. Some have more social power and influence than others. They are said to be dominant, and the structure of the relative power and influence of a group's individuals is called a **dominance hierarchy.** In addition, most primate species recognize a special status for females with infants, and these mother-child units are well protected by other members of the group, even those that are not directly related to them (Figure 7.7). Among chimpanzees and baboons, we even see lasting relationships that can only be described as friendships.

Primate social groups are maintained through communication. Primates have large repertoires of vocalizations, facial expressions, and body gestures. Touch is also an important form of communication among primates and often takes the form of **grooming,** an activity that serves not only the practical purpose of removing dirt and parasites but also as a source of reassurance to maintain group harmony and unity (Figure 7.8).

dominance hierarchy Individual differences among group members in terms of power, influence, and access to resources and mating.

grooming Here, cleaning the fur of another animal, which promotes social cohesion.



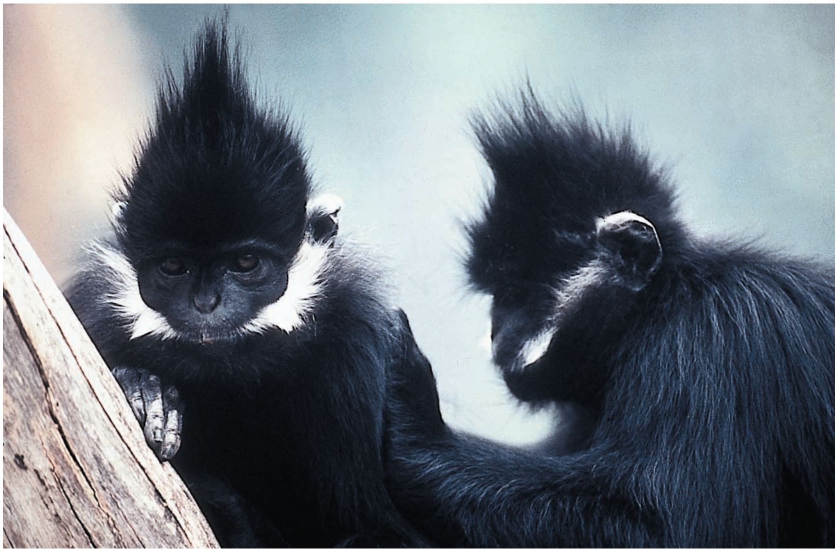


FIGURE 7.8
Primate communication and grooming. (*Top*) A chimp exhibits a *pant-hoot,* a call used when a food source is found, when two groups join together, or to communicate over distances. (*Bottom*) Grooming serves not only to rid these Francois's langurs (monkeys from Southeast Asia) of parasites and dirt but also to maintain group unity and harmony.

The Primate Adaptive Strategy

It is important to acknowledge the environment to which the primates are adapted. The basic primate environment is arboreal. To be sure, several species—gorillas, for instance—spend more time on the ground than in the branches, and we humans are thoroughly terrestrial. But the majority of primates spend most of their time in the trees, and the primate traits in the preceding discussion all evolved in response to an arboreal environment. Even the partially and completely terrestrial primates possess features that are variations on the arboreal adaptive theme. So, we may define primates in the following way:

> The primates are mammals adapted to an arboreal environment through well-developed vision, manual dexterity, and large, complex brains; their adaptation relies on learned behavior, which is aided by the birth of few offspring at a time and the direct and extensive care of those offspring during a long period of dependency while they are socialized into groups based on differential relationships among individuals.

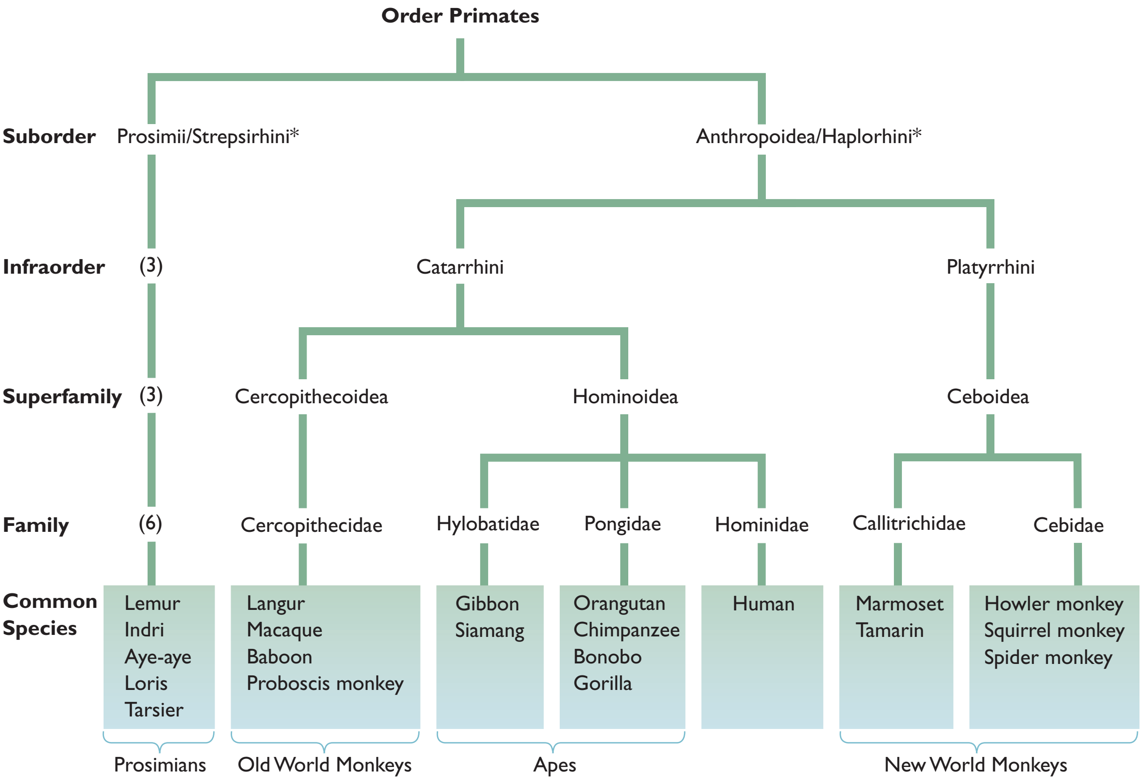
Such a complex group of organisms requires a lengthy description.

A SURVEY OF THE LIVING PRIMATES

Figure 7.9 is a traditional taxonomy of the approximately 200 to 300 species of living primates. For the sake of space, some categories are indicated only by the number of groups within them; for instance, there are six families of prosimians. One of the first things you should notice are the new categories here as compared with those shown in Table 7.1. *Suborder*, *infraorder*, and *superfamily* have been added between the traditional Linnaean categories of *order* and *family*. (A complete taxonomy of insects, for example, a class with over 750,000 *known* species, is, as you can well imagine, incredibly complex.)

Prosimians

The order Primates is traditionally divided into two major suborders, Prosimii and Anthropoidea. Prosimians ("pre-apes") represent the most primitive primates, that is, those that most closely resemble the earliest primates. At first widespread, prosimians were pushed into marginal areas as newer, more adaptively generalized primates evolved. Some modern prosimians live on the mainlands of Africa, India, and Southeast Asia and


Order Primates
Suborder
Prosimii/Strepsirhini*
Anthropoidea/Haplorhini*
Infraorder
(3)
Catarrhini
Platyrrhini
Superfamily
(3)
Cercopithecoidea
Hominoidea
Ceboidea
Family
(6)
Cercopithecidae
Hylobatidae
Pongidae
Hominidae
Callitrichidae
Cebidae
Common Species
Lemur
Indri
Aye-aye
Loris
Tarsier
Langur
Macaque
Baboon
Proboscis monkey
Gibbon
Siamang
Orangutan
Chimpanzee
Bonobo
Gorilla
Human
Marmoset
Tamarin
Howler monkey
Squirrel monkey
Spider monkey
Prosimians
Old World Monkeys
Apes
New World Monkeys

*See text for explanation.

FIGURE 7.9
A primate taxonomy using traditional categories. The numbers in parentheses refer to the number of groups in that category.

on the isolated islands of Southeast Asia, but the majority inhabit the island of Madagascar (Figure 7.10).

The forty or so living species of prosimians exhibit a number of differences from the general primate pattern. About half of the prosimian species are nocturnal and so lack color vision. They have large eyes that can gather more light, as well as better than average senses of smell and hearing (Figure 7.11). To aid their olfactory sense, they have a protruding snout with a large smell receptor area (the mucous membranes within the nose) and a moist, naked outer nose (like that of a dog or cat) to help pick up the molecules that make up olfactory signals. Prosimians do have the stereoscopic vision characteristic of primates, because they need to judge distances in bushes and trees, and their three-dimensional vision helps them catch insects, a favorite food of many prosimian species.

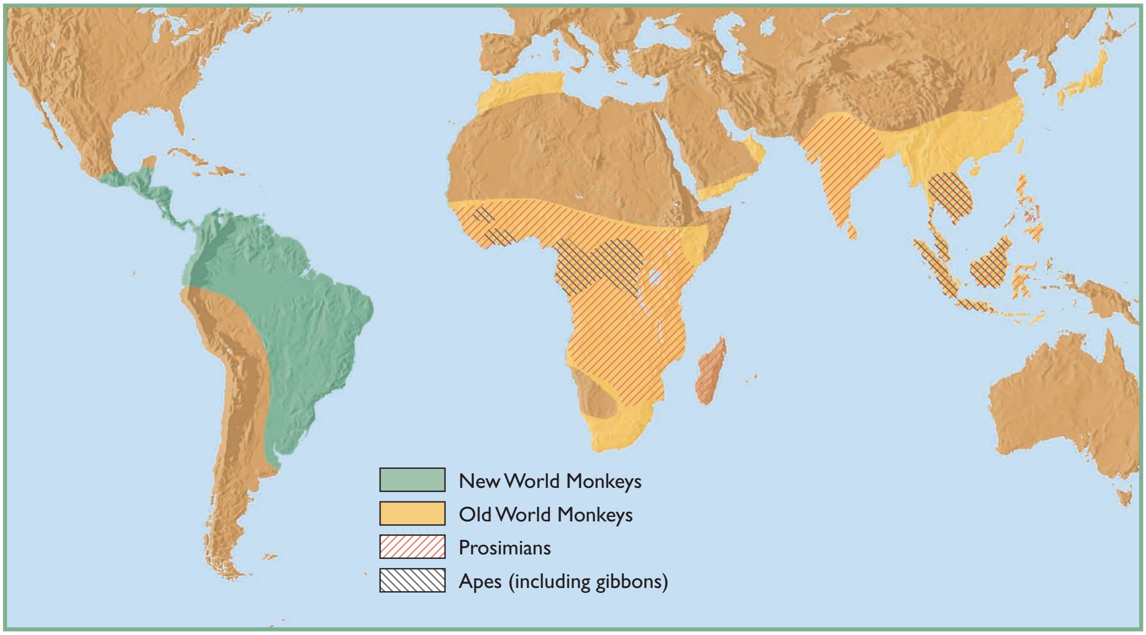


FIGURE 7.10
Distribution of living nonhuman primates.

Prosimians have prehensile hands and feet, but the opposability of their thumbs is limited. Many can only touch the thumb with the other four digits together; their digits don't move independently. Some prosimians have claws instead of the typical primate nails on a couple of fingers or toes. These are known as *grooming claws* and are used both for that purpose and to help acquire food.

A few species of lemurs from Madagascar give birth to twins or even triplets on a regular basis. Transporting the infants through the trees, however, is no problem because an adult male or an older sibling often helps the mother carry and care for her infants. At other times, the infants are kept in a nest.

A particularly interesting primate is the tarsier of Southeast Asia (Figure 7.12). Weighing just 4 to 5 ounces, this little insect eater has powerful hind limbs for jumping, enlarged fingertips and toetips for added friction, and the ability to turn its head 180 degrees in either direction, like an owl. Its name comes from its elongated ankle (or *tarsal*) bones, which make its legs look as if they bend too many times.

Because of its flat face, upright posture when clinging to trunks and branches, lack of the moist, naked nose of other prosimians, and some recent genetic comparisons, some authorities suggest placing the tarsier in

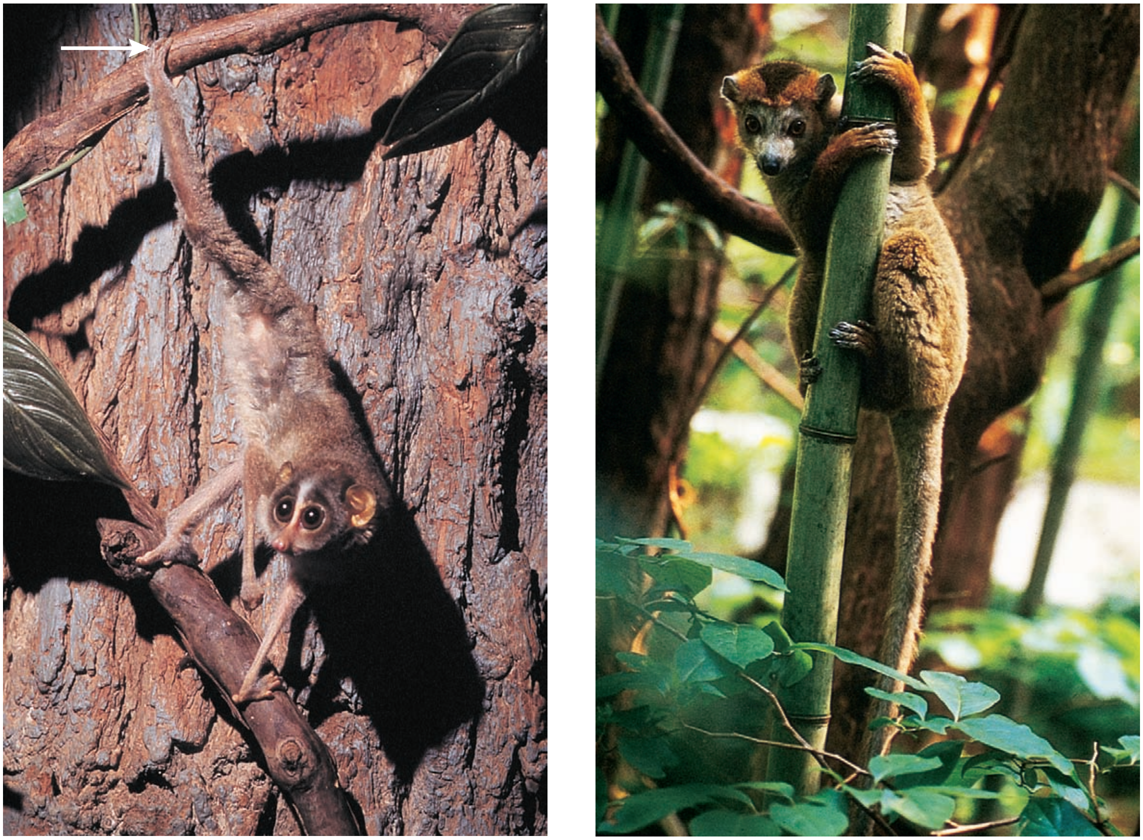


FIGURE 7.11
Two prosimians. The slender loris of India and Sri Lanka (*left*) has the large eyes and moist, naked nose characteristic of this suborder. Note also the prehensile hands and feet and the grooming claw on one toe of the foot at the top of the picture (*see arrow*). The crowned lemur of Madagascar (*right*) displays a posture that is typical of the locomotor pattern called *vertical clinging and leaping*. All the Madagascar primates are endangered.

the second primate suborder, Anthropoidea. Some go further. Focusing on the fact that all prosimians have the moist nose and anthropoids do not, they suggest dividing order Primates into suborders based on that trait. The former prosimians would thus be in suborder Strepsirhini ("nose with curved nostrils"), and the anthropoids would become suborder Haplorhini ("simple nose"). The latter group would include the tarsier because of its nose, color vision, and other traits.

Anthropoids

The anthropoid ("humanlike") primates include monkeys, apes, and humans. Suborder Anthropoidea is further divided into two infraorders,

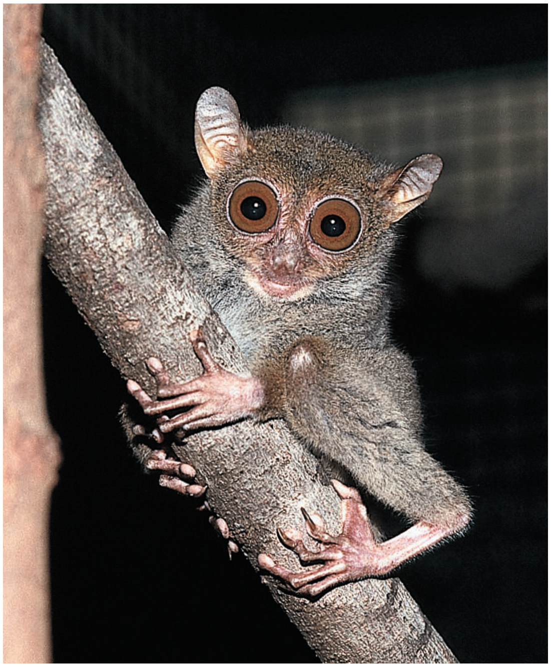


FIGURE 7.12
Philippine tarsier. Note the huge eyes (each eyeball is as big as the entire brain) for nocturnal vision, the enlarged fingertips and toetips, and the powerfully built legs with elongated ankles.

Platyrrhini and Catarrhini. This division is based on a geographic separation of early primates into a Western Hemisphere (or New World) group and an Eastern Hemisphere (or Old World) group. All the New World platyrrhine primates are monkeys. The Old World catarrhine primates comprise monkeys, apes, and humans. Despite the fact that humans now inhabit the entire globe, we first evolved in the Old World, in Africa.

Several features distinguish New World from Old World primates. The most obvious is the nose. *Platyrrhine* means "broad-nosed," and the noses of the Central and South American monkeys have widely spaced nostrils separated by a broad septum (Figure 7.13). By comparison, *catarrhine* is translated "hook-nosed." The typical Old World nose has closely spaced nostrils that face downward. Just look in the mirror.

New World and Old World anthropoids also have different dental formulas, that is, the number of each type of tooth in each quadrant of the mouth. Old World anthropoids have two incisors, one canine, two premolars (bicuspids), and three molars. This is written as $\frac{2.1.2.3}{2.1.2.3} \times 2 = 32$. Some

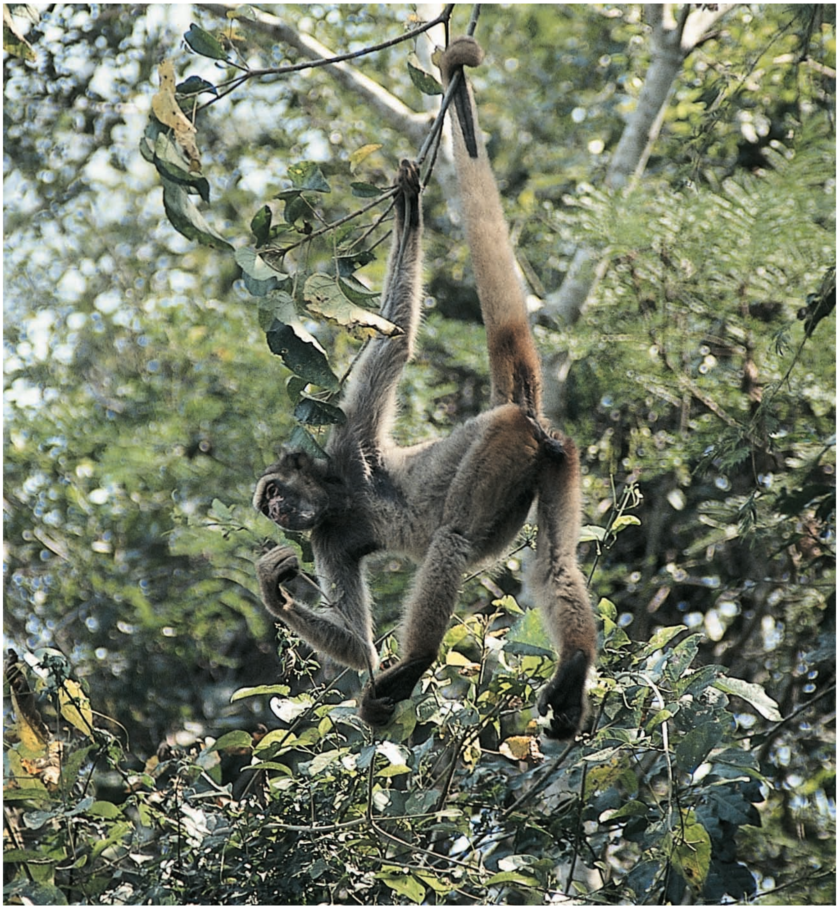


FIGURE 7.13
Northern woolly spider monkey, a platyrrhine primate from Brazil. Note the prehensile tail with the bare strip of skin on the inner surface to enhance its grasping ability. Note also the typical platyrrhine nose (see also Figure 7.6 *bottom left*).

of the New World anthropoids have four additional premolars: $\frac{2.1.3.3}{2.1.3.3} \times 2 = 36$. Other New World anthropoids have four additional premolars but four fewer molars: $\frac{2.1.3.2}{2.1.3.2} \times 2 = 32$.

Because New World monkeys are almost entirely arboreal, they have evolved long limbs, and some have clawlike nails. Several species also have evolved prehensile tails and thus effectively have five grasping limbs. No Old World monkey evolved this adaptation. Finally, two groups of platyrrhines, the marmosets and tamarins, normally give birth to twins.

The Old World primates are divided into two superfamilies. The monkeys of Europe (now limited to Gibraltar), Africa, and Asia make up superfamily Cercopithecoidea. Apes and humans are in superfamily Hominoidea, which is further divided into three families.

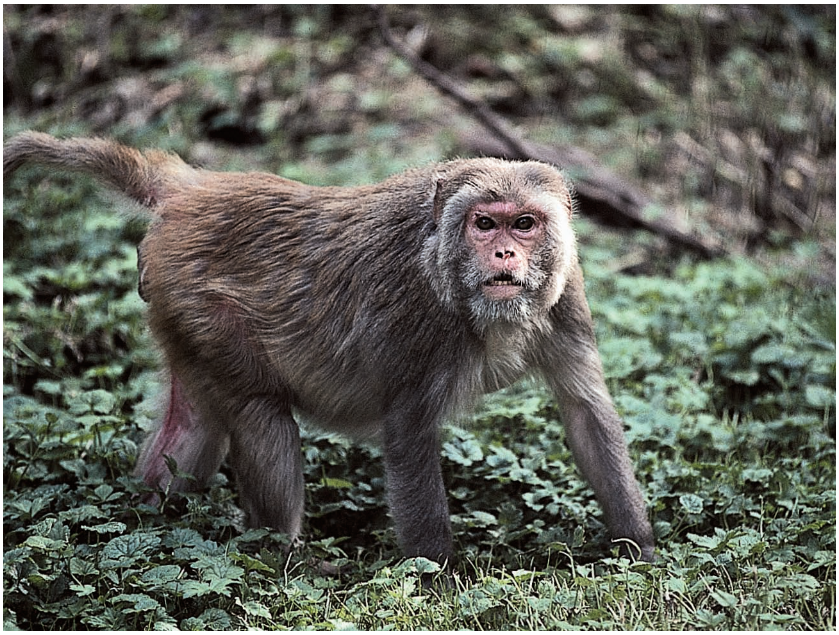


FIGURE 7.14
Rhesus monkey, a catarrhine primate from Asia. Note the more closely spaced nostrils as compared to the platyrrhine (New World) monkey in Figure 7.13. (See also Figure 7.6, *top left* and *right* and *bottom right,* and Figure 7.8, *bottom*.) The rhesus has been important in medical and behavioral experimentation. The Rh blood factor was named after it.

There are 100 or more species of cercopithecoids (Figure 7.14). They have the nasal shape and tooth number of all Old World primates, and most have tails. Males tend to be larger than females, a trait not common in New World species. Also unlike the platyrrhines, the Old World monkeys have fully opposable thumbs. The monkeys of the Eastern Hemisphere seem more adaptively flexible than those of the New World. At home in the trees, many cercopithecoids are equally comfortable on the ground. They live everywhere from the deserts of Africa and the Middle East to the mountains of northern Japan.

Superfamily Hominoidea contains the larger, tailless primates. The hominoids—the apes and humans—are generally larger than the monkeys and have larger brains, both relatively and absolutely. Their brains also have larger neocortexes, meaning that the hominoids are more intelligent, as we have defined that term. Finally, a series of traits make the hominoids good suspensory climbers and hangers; they are adapted to an arboreal environment through the ability to climb and hang from branches with their arms. The traits behind this ability are a flexible shoulder joint, a more posterior shoulder blade than in monkeys, and a stronger collarbone (clavicle) for added support. Although modern

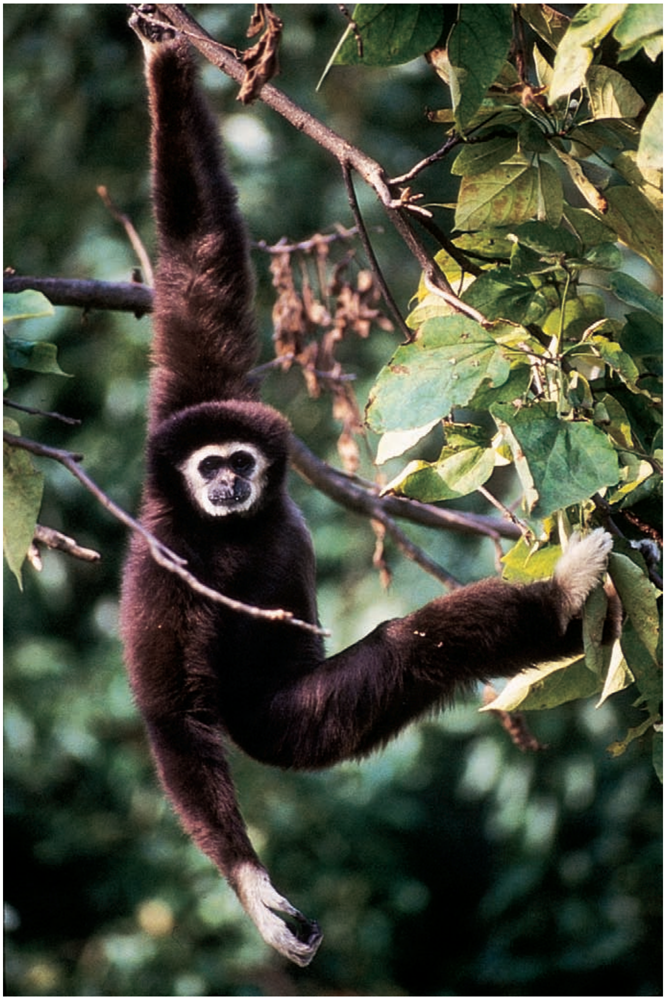


FIGURE 7.15
White-handed gibbon from Southeast Asia. Note the long, hooklike fingers and the grasping feet.

humans do not display the ability to climb or hang using the arms as often or as well as the apes, we still possess it, as demonstrated by gymnasts on the high bar or rings.

Family Hylobatidae includes the gibbons and siamangs of Southeast Asia and Malaysia. Sometimes referred to as *lesser apes,* they are noted for their brachiating mode of locomotion (Figure 7.15). They also have an unusual social organization for primates. Male and female hylobatids form a monogamous pair, though not neccessarily a permanent one.

There are four species collectively known as the *great apes* (Figure 7.16): the orangutan of Southeast Asia and the gorilla (possibly two

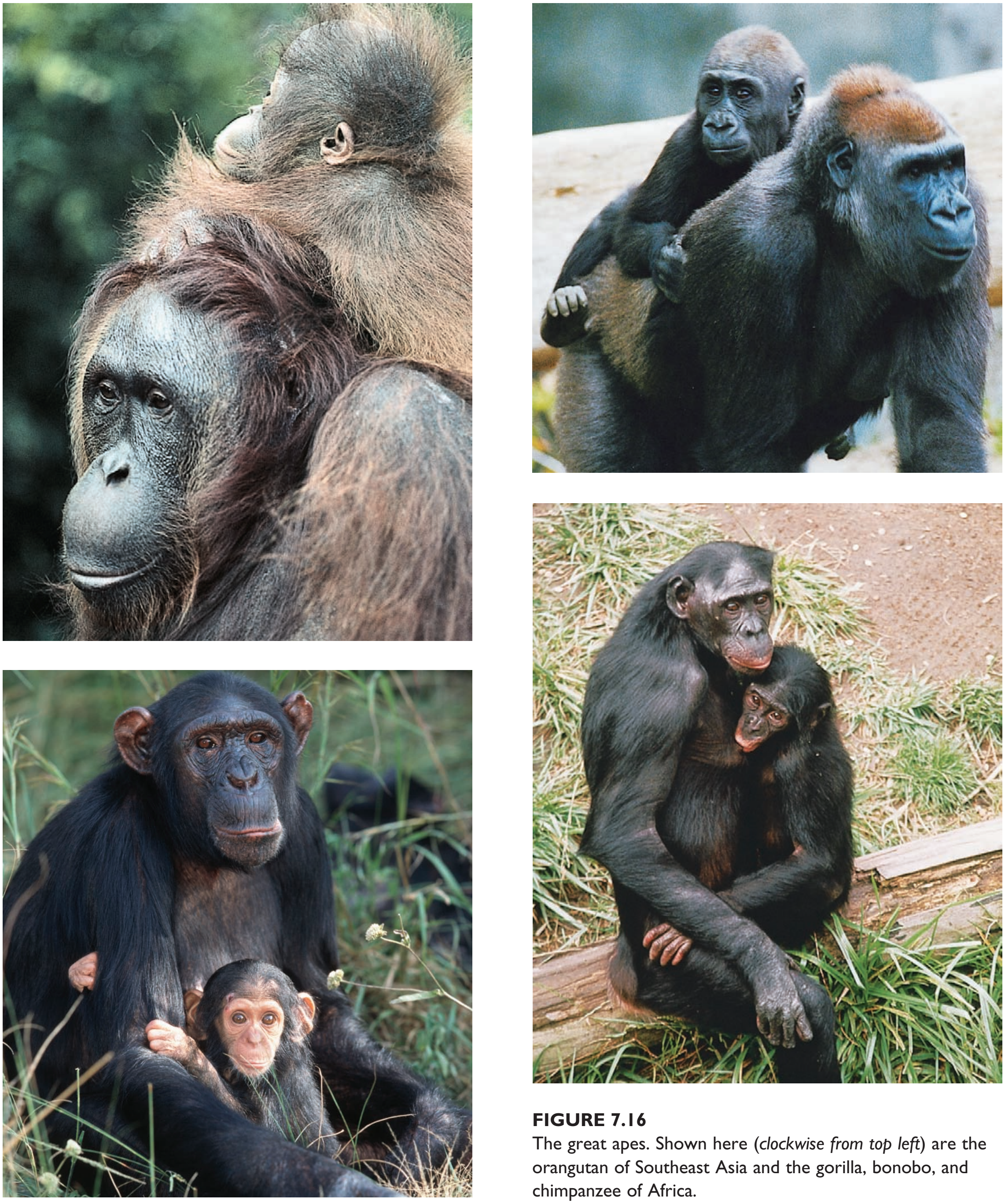


FIGURE 7.16
The great apes. Shown here (*clockwise from top left*) are the orangutan of Southeast Asia and the gorilla, bonobo, and chimpanzee of Africa.

species), chimpanzee, and bonobo of Africa (all traditionally in family Pongidae).

The great apes are large (a male gorilla in the wild may weigh 450 pounds), with heavy, powerful jaws used for eating a wide range of fruits, nuts, and vegetables. Chimps and bonobos also eat meat on occasion. The apes are quadrupeds, although chimps, gorillas, and especially bonobos are fairly good at upright walking for short distances. Orangutans are solitary, but the other apes live in social groups marked by some degree of dominance but otherwise with fairly loose organization and changeable group membership.

The apes have relatively large brains; a large chimp may have a brain half the size of the smallest modern human brain. Apes are intelligent. They have, for example, an intimate knowledge of a large number of food sources, many of which ripen seasonally or grow in limited areas.

Some chimpanzees can make simple tools; the best known is their termite "fishing stick," a modified twig or blade of grass they insert into a hole in a termite mound and wiggle around to stimulate an attack by the insects. The termites cling to the "invader," and the chimps draw out a tasty meal (Figure 7.17). Other chimps have been seen using rocks to break open hard-shelled nuts. Chimps are also known to cooperatively hunt small animals, including other primates, and meat is the one food source that chimps will share with one another (see Chapter 8). And in 2007 it was reported that some chimps in Senegal had been seen sharpening sticks with their teeth to use as spears for stabbing and extracting galagos (also called *bush babies*, small nocturnal primates) from their daytime holes in trees.

Finally, apes have a large repertoire of calls, facial expressions, and body gestures with which they communicate information, mostly about emotional states. Although this form of communication is nothing like human language, some individuals from all the great ape species have been taught to use nonvocal versions of human languages, most notably American Sign Language (Ameslan), developed for the hearing impaired. It is said by some researchers that with this skill they can communicate at the level of a 4- or 5-year-old human.

One branch within superfamily Hominoidea is family Hominidae (see Figure 7.1 and Figure 7.9). This includes all living and extinct species of habitually bipedal primates. Let's now look at the traits of this group.

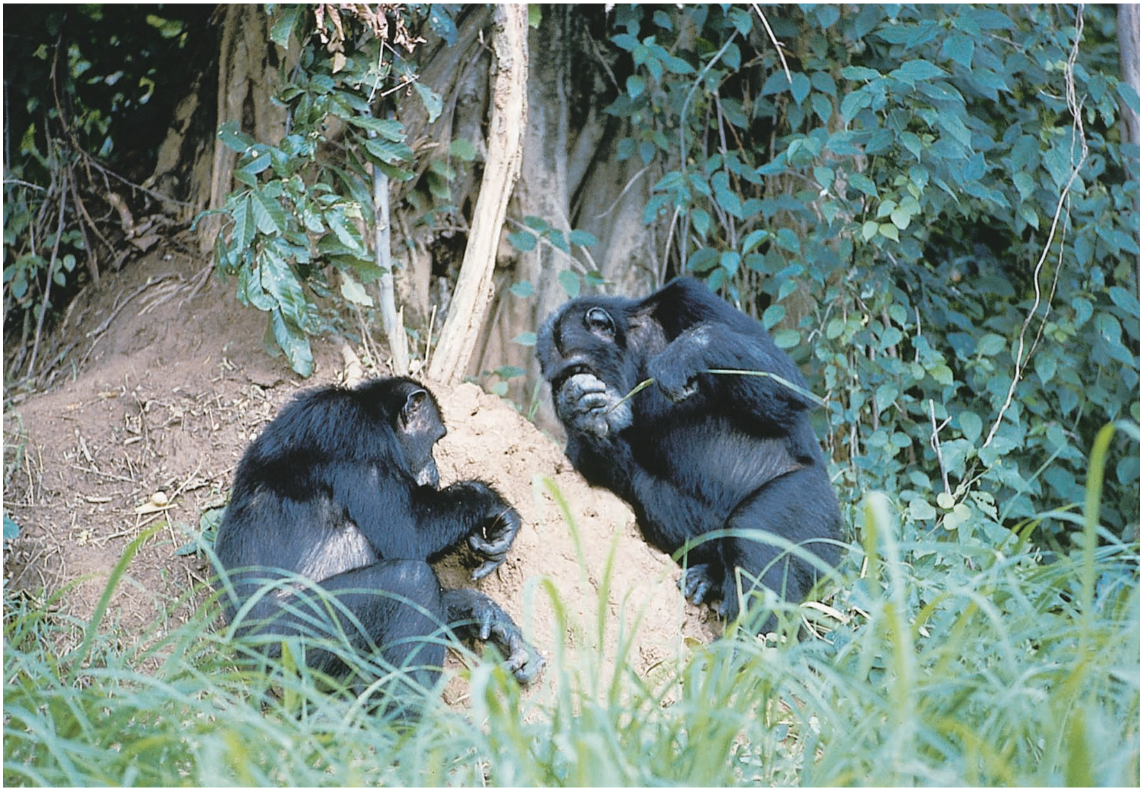


FIGURE 7.17
Chimps using tools they have made to extract termites from their mound.

THE HUMAN PRIMATE

Each of the 200 to 300 living primate species has its own unique expression of the primate adaptive strategy. Humans are no exception. Let's describe ourselves by using the same categories with which we characterized primates in general. (See Table 7.3 for a summary.)

The Senses

Our senses are essentially the same as those of the anthropoid monkeys and the apes. There may be some minor differences, but basically all these species hear, smell, feel, and, especially, see the same world.

TABLE 7.3
The Features of the Human Primate

Brain	*Vision*	*Face*	*Hands\Feet*	*Limbs*	*Reproduction*	*Behavior*
1,000–2,000 ml	As in anthropoids	Flat	No prehensile feet	Arms most flexible	Longest period of dependency	Culture
3 times expected size			Most dexterous hands	Habitual bipedalism	Differences in sexuality	

Movement

Bipedalism is the characteristic that in broad evolutionary perspective defines the hominids. We are the only living primate that is habitually bipedal, and we have been for over 4 million years. (Our big brains came along much later.) The bones and muscles of our back, pelvis, legs, and feet are all structured to balance us and hold us upright (see Figure 9.5). Because our legs are the limbs of locomotion, they are longer and more muscular than our arms—just the opposite of the arms and legs of the apes. Completely freed from locomotor functions, our hands have become organs of manipulation. We have the most precise opposability of any of the primates and the relatively longest and strongest primate thumb.

Reproduction

Like most primates, we usually have one offspring at a time. Although we are not the largest living primate (the gorilla is), we have the longest period of postnatal dependency, and we take the longest time to mature. Chimps, for example, reach sexual maturity at about 9 years and physical maturity at about 12. For humans, the averages are 13 and 21. In addition, we are born more helpless than other primates.

Our sexual behavior, too, is different. Most other primates, like most mammals, engage in sexual activity, for the most part, only when it can lead to reproduction. Thus, mating tends to occur when a female has ovulated, that is, when an egg has matured and is ready to be fertilized. She undergoes hormonal changes that make her sexually receptive and lead her to solicit male attention by giving off sexually stimulating signals. During this time, the female is said to be in **estrus** (popularly, “in heat”). In many mammals, the estrus signals are in the form of olfactory stimuli; in some primates, they are also visual (Figure 7.18).

Humans, of course, have lost the signals of estrus, a condition best referred to as *nondetectable ovulation* (A. Fuentes, personal communication). Human males don’t automatically know when a human female is fertile.

estrus In nonhuman primates, the period of female fertility or the signals indicating this condition.

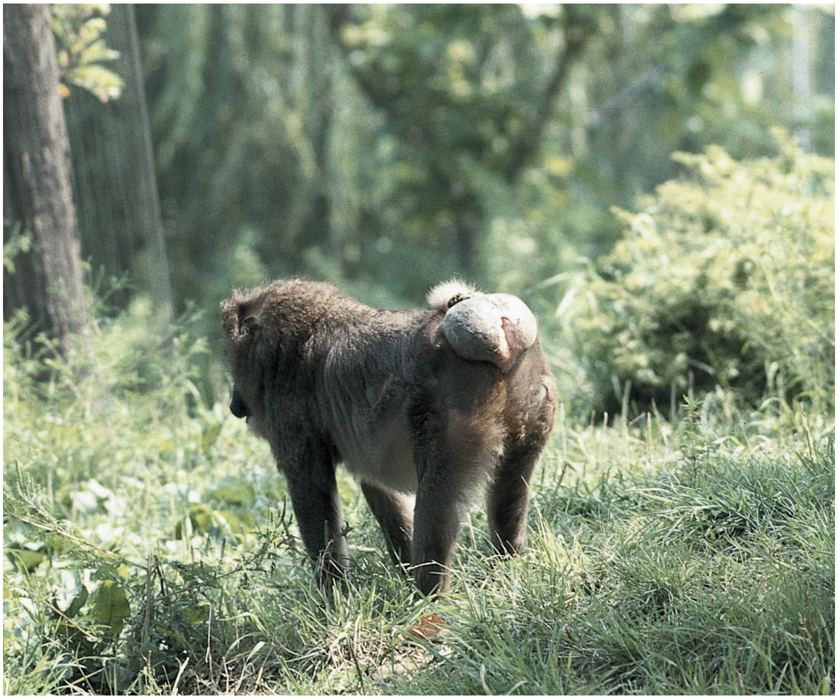


FIGURE 7.18
Baboon in estrus. The skin around this female's genital area is swollen, a clear visual sign that she is fertile and sexually receptive. In baboons and other primates, this area may also be brightly colored.

Contemporary Reflections

What Is the Status of Our Closest Relatives?

In a nutshell, the answer is, not good. In 2008 the International Union for Conservation of Nature and Natural Resources (www.redlist.org) recognizes 634 species of primates.* Of these, 64 are listed as "critically endangered," 141 as "endangered," 98 as "vulnerable," and 37 as "near threatened." The rest are "least concern," or "data deficient" (neither of which are necessarily good signs).

And it's getting progressively worse, especially in Africa and especially among the great apes. An estimated 80 percent of the world's gorillas and most chimpanzees live in the West African countries of Gabon and the Republic of Congo. In Gabon, the populations of those species have decreased by more than half over the last twenty years. Five thousand gorillas in a sanctuary in Congo died in 2003 and 2004. At its present rate of decline, the bonobo will be extinct in the wild in a decade. In the mountains to the east of those countries, the population of the rare mountain gorilla (made famous by the book and film *Gorillas in the Mist*) is thought to be down to fewer than 650 individuals. In 2007, seven of these gorillas were murdered, for no apparent reason.

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*There are not that many acknowledged species, so some of these are certainly named subspecies or even just named populations.

What is causing this disastrous decline? Worldwide we humans threaten the primates, as well as other endangered species, through our overpopulation, depletion of resources, warfare, habitat destruction, pollution, hunting, and other direct exploitation of innumerable species, both plant and animal. In the case of the African apes, the effects of hunting have been recently exacerbated by the "bushmeat" trade, targeting any number of large native animals, including chimpanzees, bonobos, and gorillas. The encroachment of logging and mining into these animals' habitats (particularly in Congo, which is rich in coltan, an ore used in the production of cell phones and laptops) has brought an influx of workers who subsist on the meat of whatever animals are available to hunt, whether endangered or not. Elsewhere, local peoples in need of food in their poverty-stricken countries are also turning to hunting. And most egregiously, and the main motivation for hunting, there is a lucrative commercial market for bushmeat in African cities and towns as well as abroad. Some believe that hunting caused the first recorded primate extinction—of the wonderfully named Miss Waldron's red colobus, an African monkey.

Related to the bushmeat trade are two serious threats to humans—the AIDS virus (see Chapter 12) and the virus that causes Ebola, the hemorrhagic fever whose origin is still unknown (Bermejo et al. 2006). Ebola decimated the gorillas at the sanctuary in Congo and is now spreading toward a national park that has one of the largest, densest ape populations in the world. Outbreaks of the disease in apes coincide with outbreaks in human populations, so it is likely that humans are contracting Ebola from apes, largely as a result of hunting and eating them. It's unclear whether the apes are transmitting the disease to one another or are, because there are more and more humans in the forests, being forced into closer contact with the source of the virus (hypothesized to be bats, mice, or birds). But we do know that outbreaks have occurred among apes in regions remote from human habitation as well.

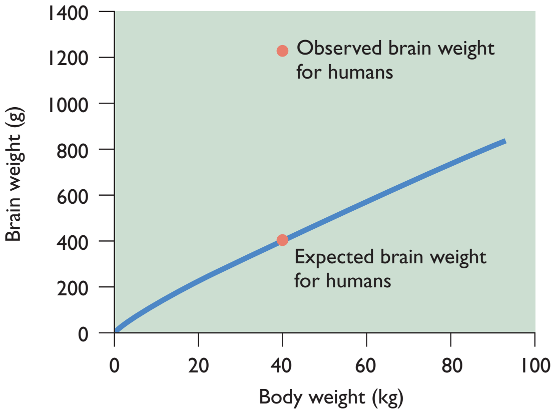
The debate now centers on what action to take. The status of these western gorillas has been heightened to "critically endangered." Also needed is a "massive investment" in law enforcement to prevent hunting and stem the bushmeat trade. As for Ebola, some have suggested transporting apes to a safe area or otherwise dividing infected groups from noninfected groups. If, however, the apes are continually contracting the disease from its still-unknown source, these measures won't do much. There is an experimental vaccine that works on monkeys, but it still requires testing, and administering it to wild animals would be a difficult task.

The prospects, in other words, don't look good—either for the apes of West Africa or, in the long run, for the world's other primates and all the other endangered species of life. At times, the situation seems hopeless, but various organizations are working tirelessly to prevent the local zoo from ultimately being the *only* place to see the apes and other species. For more information on the crisis, what is being done, and how we can help, see http://pin.primate.wisc.edu and click on "Conservation," under the heading "About the Primates." Also see www.unep.org/grasp for information on the United Nations Great Apes Survival Partnership. To paraphrase Gandhi, whatever we do might be insignificant, but it is very important that we *something*.

This may seem a rather inefficient way to perpetuate the species, but as we are all aware, humans have replaced unconscious, innate sexual signals with sexual consciousness. Sexuality has become part of our conscious thought, tied up with all the other reactions and attitudes and emotions we have toward other members of our species and toward ourselves. You might say we are potentially continually in estrus. Although humans exhibit the most extreme form of this reproductive behavior, we will see it foreshadowed, in the next chapter, in some of our close relatives.

FIGURE 7.19 Relationship between body weight and brain weight in primates. The line indicates the average relationship among various primate species excluding humans. The two dots show expected and observed brain weight for humans. Our brains are three times the weight expected if we followed the typical primate curve.

(Data from Harvey et al. 1987; figure and caption from Relethford 2008.)



Intelligence

We are clearly the most intelligent primate, as we have defined that term. We can store, retrieve, and process more information in more complex ways than all the other primates. Our cultural behaviors—our languages, societies, belief systems, norms of behavior, and scientific knowledge—all attest to these abilities. Our intellect is made possible by our large, complex brain, especially our neocortex, the outer layer where abstract thought takes place. Our brains are, in fact, three times the size expected for our body weight as primates (Figure 7.19).

Behavior Patterns

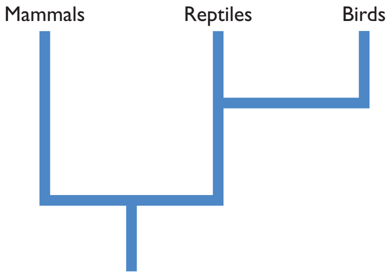
Like most Old World primates, humans live in societies that are based on the collective conscious responses of a group of individuals. The difference is that our groups are structured and maintained by cultural values—ideas, rules, and behavioral norms that we have created and shared through complex **symbolic** communication systems.

ARE WE HOMINIDS OR HOMININS?

Do any reading in human evolution and you'll no doubt see both terms used to refer to us, that is, modern humans and our ancestors, the habitually bipedal primates. Which name is correct? Why does it matter? The question goes back to the difference between phenetic and cladistic taxonomies, introduced in the first section of this chapter.

symbolic Here, a communication system that uses arbitrary but agreed-upon sounds and signs for meaning.

A cladistic taxonomy establishes actual patterns of branching by looking at "shared, derived characteristics," unique features inherited by multiple groups from a common ancestor. Groups that share a number of such features are close relatives, regardless of what other traits might distinguish them from one another. In many if not most cases phenetic and cladistic trees will agree, but not always. Thus, in a famous example, even though birds, reptiles, and mammals have always been classified in separate taxonomic classes (see Tables 7.1 and 7.2) with equivalent status, we know that birds and reptiles are more closely related. This is because birds are descended from a type of dinosaur, an extinct reptile; we know this because of features shared by birds and dinosaurs that are possessed by no other group. A family tree would look like this:



Technically, then, birds should be included in class Reptilia. The problem here is that birds have diverged so much from reptiles, even though evolved from one group of them, that the birds are distinctly different and inhabit a different adaptive zone. Thus, some specialists, while acknowledging the tree drawn above, retain birds within their own class, Aves, because, after all, a classification is a human construct that, in the words of anthropologist Jonathan Marks (2011:195) "facilitates communication among scientists," and is "a framework that imposes order upon species in nature" by summarizing "the overall relationships" among organisms. No one classification system can be expected to fully and with complete accuracy depict the complexities of nature.

How does this relate to us? Look back at the inferred family tree of the hominoids (apes and humans) in Figure 7.1, where apes are pongids and humans are hominids. The tree itself may not be accurate. Some (but not all) recent genetic evidence suggests that chimps (including bonobos) and humans are more closely related to one another than either is to the gorilla, despite appearances. The orangutan, we know, is more distantly related. Thus, the currently accepted tree looks like Figure 7.20.

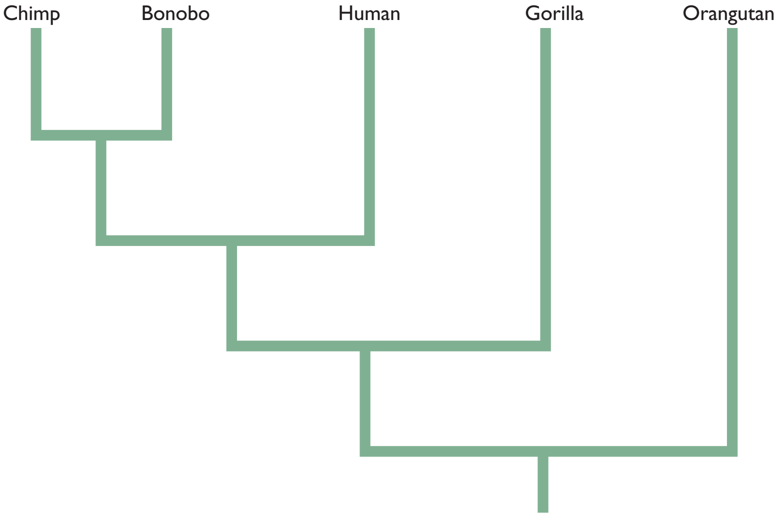


FIGURE 7.20 Evolutionary tree based on cladistic analysis.

With a phenetic tree, there's a branch every time a classification distinction is made (see again Figure 7.1). With cladistics, every time there's a branch (technically, a *node*) a new category must be established. (This results in a proliferation of names, so much so that insect taxonomists now use a number and letter system instead of trying to dream up new names for each of thousands of nodes.) Thus, one of several schemes for the presumably accurate tree is in Figure 7.21.

It has become common, if not a trend, then, to consider humans and the African apes as members of family Hominidae (the hominids) and humans as members of tribe Hominini (the hominins). But there are problems with this (aside from the difficulty in distinguishing the two words when speaking them!).

First, all the genetic data do not point unequivocally to the human-chimp-gorilla relationship as in Figure 7.20. Different studies of different portions of the three genomes provide different results. And to be sure, the relationship in the figure is not supported by the anatomy of the three species in question, which means that genetics (which, as you will recall, we are still working on understanding) is given priority over phenotype and adaptive mode.

Second, humans here are like the birds. We are certainly evolutionarily part of the group made up of the African apes but we have (for reasons we'll cover in upcoming chapters) diverged quickly and so much from them that we inhabit a completely new adaptive zone. Even with our close genetic relationship to chimps, we are a very different sort of creature. Making us and the chimps a "sister group" as in Figure 7.21 ignores this. And recall that adaptation is the key to evolution.

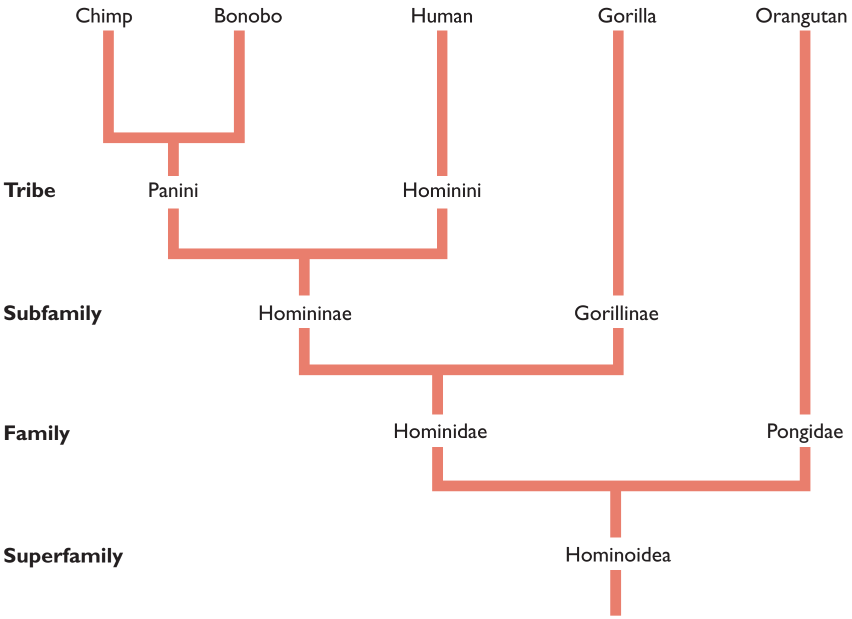

Chimp
Bonobo
Human
Gorilla
Orangutan
Tribe
Panini
Hominini
Subfamily
Homininae
Gorillinae
Family
Hominidae
Pongidae
Superfamily
Hominoidea

FIGURE 7.21
One possible taxonomic classification based on cladistic analysis. Note that new categories have had to be added.

Finally, in a cladistic tree, each new branch requires a defining set of "shared, derived characteristics." The node in Figure 7.21 labeled "Subfamily Homininae," separating the chimps and humans from gorillas, has no such set. There is no combination of traits shared by humans and chimps that is not possessed by gorillas. This classification is based strictly on genetics, which are still questionable.

Thus, and perhaps going against the tide (not to mention changing my mind on the subject from earlier), on this book I will stick with the traditional classification of humans and our direct ancestors (the habitually bipedal primates) as hominids.

SUMMARY

The study of the nonhuman primates has been a traditional aspect of biological anthropology. Humans *are* primates, after all, and the characteristics of our relatively new species have evolved out of the basic primate traits and the adaptive strategy that they facilitate. We can only fully comprehend ourselves as a biological species by understanding where we fit into the natural world.

Taxonomy provides us with a way of naming and categorizing species so as to indicate their biological relationships. It also gives us an idea as to the evolutionary relationships among species. At present, there are two major schools of thought about taxonomy. One (phenetic) names and classifies according to comparisons of phenotypic features and adaptive behaviors. The other (cladistic) uses the actual evolutionary pattern of branching. This book will recognize a phenetic classification for our small section of the primate family tree and consider us as hominids.

The primates are one of nineteen orders of mammals. They may be characterized as being adapted to arboreal environments through manual dexterity, visual acuity, and intelligence. There are 200 to 300 living species of primates, each a unique manifestation of the general primate theme. The human primate's major uniqueness is its form of locomotion; we are the only primate that is habitually bipedal, a trait that evolved more than 4 mya. Since then, our other distinguishing feature has evolved—our big brain, capable of such complex functions that we can create our own adaptive behaviors, expressed as our various cultural systems. It is to the possible precursors of our behaviors that we will turn next.

QUESTIONS FOR FURTHER THOUGHT

1. Birds evolved from a group of small bipedal dinosaurs. Cladistic analysis justifies lumping birds and dinosaurs into the same taxon. Some have taken this to mean that the caged parakeet in your living room is a dinosaur. What do you think of this? Is your dog, then, really a wolf? Are humans a form of ape? How far can we take cladistic taxonomies in our popular nomenclature? Is there some inherent contradiction in cladistic taxonomies, or can you see a resolution?
2. The primates come in a wide variety of shapes and sizes and live in a broad range of environments. It's tempting to attribute this adaptive success to the primates' big brains. But it's more complex than that. Thinking about the processes of evolution, speciation, adaptive radiation, and species selection, how would you account for the seeming success of the primate order?
3. Given the problems that now beset the human species on the African continent—AIDS and other diseases, poverty, civil unrest, and warfare—how can we justify expressing so much concern for the plight of the nonhuman primates, much less expending money and time on their behalf? Are these separate concerns that should be considered in order of priority? Or are they actually inextricably linked?

KEY TERMS

taxonomy
phenetic
cladistic
stereoscopic vision
quadrupedal
bipedal
prehensile
brachiation
opposability
postnatal dependency
intelligence
dominance hierarchy
grooming
estrus
symbolic

SUGGESTED READINGS

Noel Rowe's *The Pictorial Guide to the Living Primates* is a beautifully illustrated and informative reference to all living primate species. For a look at the endangered lemurs of Madagascar, see the article in the August 1988 *National Geographic* by primatologist Alison Jolly: "Madagascar's Lemurs: On the Edge of Survival." The National Geographic Society has also produced a beautifully illustrated book on the great apes: *The Great Apes: Between Two Worlds*, by Michael Nichols, Jane Goodall, George Schaller, and Mary Smith, not only discusses the four species of apes but also talks about the scientific studies conducted on them in the wild, as well as the dangers they now face from their close relative.

More on the linguistic abilities of the apes can be found in "Chimpanzee Sign Language Research," by Roger and Debbi Fouts, and in *The Nonhuman Primates*, edited by Phyllis Dolhinow and Agustín Fuentes. A more detailed treatment is Roger Fouts's *Next of Kin*.

A comprehensive and readable book comparing humans with other primates is Richard Passingham's *The Human Primate*. For an interesting though somewhat speculative discussion of the evolution of the human brain, try Carl Sagan's Pulitzer Prize–winning *The Dragons of Eden*.

For more on cladistics, see "Evolution by Walking," by Stephen Jay Gould, in the March 1995 *Natural History*, and "Why Cladistics?" by Eugene Gaffney, Lowell Dingus, and Miranda Smith, in the June 1995 issue of the same magazine. For a very detailed discussion of taxonomic models, see Mark Ridley's *Evolution*, third edition, Chapter 14. A good discussion of the debate within taxonomy and its implications for human evolution is in Jonathan Marks's *The Alternative Introduction to Biological Anthropology*.

For conservation information, try the Web sites listed in this chapter's "Contemporary Reflections" box, as well as www.duke.edu/web/primate.

I'll recommend some more books on the behavior of humans and our fellow primates in the next chapter.

8 CHAPTER

Primate Behavior and Human Evolution

Often I have gazed into a chimpanzee's eyes and wondered what was going on behind them.
—Jane Goodall (1990)

Just as we look to the anatomy of our close relatives to get some idea about the basic set of phenotypic traits from which we evolved, we may also look to the behavior of the other primates to gain some insight into why we behave the way we do. Because we share common ancestors, some of our behavior patterns—just like some of our physical features—may be variations on the same evolutionary theme.

In this chapter we will look at several particularly relevant nonhuman primates, the several species collectively called baboons (genus *Papio*) and the two species of genus *Pan*, the chimpanzee and the bonobo.

We will address the following questions:

How did behavior evolve, and how do we study it?

What are some of the relevant behaviors of our close relatives?

What do they tell us about the evolution of behavior in the hominids?

BEHAVIORAL EVOLUTION

Studying nonhuman primate behavior to shed light on human behavior is based on the same premise as studying the physical traits of nonhuman primates and comparing them with our own: we share a common heritage with the other primates and so have inherited our shared features from the same source, a common ancestor. It is not a coincidence, for example, that all the primates have prehensile hands. Thus, we gain some perspective on our prehensile hands by fully examining the prehensile appendages of species with whom we share an ancestor that was the source of the trait.

How Do Complex Behaviors Evolve?

Just as organisms pass on anatomical and physiological features in their genes, they also pass on behavioral characteristics. In some groups—ants, for example—whole behavioral repertoires are inherited. Ants rely completely on built-in instinct; they don't really think or, in fact, have much of anything to think *with*. So, even though ants live in highly complex societies and act in elaborate ways, all their behaviors are coded in their genes, to be triggered by outside stimuli but with little or no flexibility or variation in their response.

Other organisms with larger and more complex brains can vary their behavior as needed to cope with specific situations. Their behavior is flexible. They have behavioral *potentials* carried in their genetic codes, and they respond to their environments by building on these potentials—taking in information from the outside, remembering it, retrieving stored information, and utilizing it in appropriate circumstances. In other words, they *think*.

The nature of the inborn behavioral potentials in complex organisms is still a matter of debate, especially when humans are the topic. Some have argued that we are born as blank slates or, in a more modern image, as computers with internal hardware but nothing programmed. The extreme opposite view says that our brains come equipped with specific behaviors that are only modified to a small degree by our individual experiences—like a computer with many application programs already in the system.

The reality is no doubt somewhere in the middle. Certainly we come into this world with some basic behavioral responses built in. Facial expressions such as smiling, the newborn's instinct to nurse, the bond between a mother and her offspring, the drives to walk upright and learn language—these are all recognized as universal in our species and as preprogrammed in our biology. But just as certainly, we are not programmed for *particular* ways of expressing these and other behaviors. Language ability, for example, may be instinctive, but the specific language you speak is learned within a specific cultural and individual context.

Thus, in complex organisms, genes for these potentials can be selected for. In humans, in particular, the behavioral potential that was the focus of selection is flexibility itself, the ability to adjust one's behavior to specific circumstances, made possible by our large brains that take in, store, allow access to, and can manipulate huge amounts of information.

How Do We Study Behavior?

If it is the case that at least behavioral themes can be inherited, then we can shed light on our behaviors by looking into those of other creatures. In doing so, however, we need to take into account the concept of shared derived characteristics (see Chapter 7) or **homologies.** In comparing the behaviors of humans and chimpanzees or bonobos, it is highly likely that a behavior is shared because it is the *same* behavior, derived by all three species from our common ancestor of 6 to 5 mya. Understanding the nature and function of that behavior in chimpanzees or bonobos is likely to provide insight into the behavior in humans.

By contrast, a specific behavior similar in humans and baboons is less likely to be a homology. Our two species have evolved independently for over 20 million years, so there is a greater chance that the behavior evolved separately, under separate environmental circumstances and perhaps for different adaptive reasons. Still, the behavior may be a variation on some *general behavioral pattern* common to the primates and inherited from an early common ancestor.

The chance of two similar behaviors being homologous decreases as we compare species that are less and less closely related. Some investigators have compared the behavior of humans with that of social carnivores such as lions, wolves, and African wild dogs (Figure 8.1). There are strikingly "human" behaviors in these species: All three hunt cooperatively. Lions from the same pride will eat from the same carcass, and mothers, of course, will bring food—sometimes still alive—back to their young. Wolves and wild dogs have complex social relationships, they use vocal and gestural signs to maintain these relationships, and both actively feed their young. Wolves, especially, are territorial. These collections of similarities, however, are probably not derived from a common ancestor but have, at most, evolved quite independently from some general mammalian traits of social interaction, care of young, and relatively large, complex brains that allow for flexibility of behavior. What we do learn from the behavior of such species is that one possible route to adaptive success for mammals is through complex social behavior and that this behavior is common in species that eat meat, especially meat from large animals. But it is only one route; other carnivores—the fox and leopard, for example—are solitary hunters. And lions, although they hunt

homology A trait derived from a common ancestor. Homologies need not serve the same function.

FIGURE 8.1
African wild dogs are known for their complex social organization, particularly evident when they prepare for and participate in a hunt.

cooperatively, do not share food in the sense that one actively gives a portion of a kill to another.

Comparing such behaviors, then, can be informative and can point out possible clusters of adaptive traits. But such comparisons must be viewed with the understanding that the more evolutionarily distant the species, the less useful the comparison. Ants live in highly complex societies, which investigators often describe in human terms (*slave, caste, queen, nurse, soldier*), but studying the social behavior of ants probably tells us nothing directly about our own societies.

We can now look at the behavior of some other species that have, to varying degrees, been used as models for the origin and evolution of our own behavior. For years, nearly all our information about the behavior of other species came from studies conducted in the artificial environments of zoos and laboratories. It wasn't until the science of **ethology**—studying creatures in the wild, under natural conditions—became popular and possible that we could see how they were *really* adapted. And only then did we begin to learn some of the truly remarkable adaptations that our fellow primates possess.

PRIMATE BEHAVIORS

Baboons

Five types of baboon live in the African woodland, desert, and **savanna,** all grouped within genus *Papio*. (Some authorities consider them to be subspecies of a single species. Others give them five different species names.) Although not as closely related to humans as are the apes, these primates have long been of interest to anthropologists because of their complex social organization and their savanna habitat—an important habitat for our early hominid ancestors (Figure 8.2).

Baboon groups range in size from 20 to 200 individuals. One of the most striking aspects of baboon behavior is the aggressive competition for dominance among males, who may be nearly twice the size of females and who are endowed with huge, sharp canine teeth (Figure 8.3). The male who is the largest, strongest, most aggressive, smartest (whatever traits are important to baboons) becomes, for a time, the dominant animal, a position recognized and acknowledged by the whole group. The dominant male is the group's leader and decision maker. He has first rights to food and often to females. He may produce the most offspring, perpetuating some of those traits that allowed him to achieve dominance. It is also the role of the dominant male and his immediate subordinates to protect the more vulnerable members of the group—the females and infants—from danger (see Figure 7.7).

Males are also, in general, dominant over females. In the hamadryas baboon of Ethiopia, males gather a group of females with whom they have exclusive mating rights, often using coercion to maintain this.

Observations of these behaviors led early investigators to depict baboon social organization as almost militaristic—centered around and totally dominated by a hierarchically arranged group of males and maintained through violent (though not always bloody) confrontations. Indeed, baboon groups have traditionally been called *troops*. The female's role was considered to be the bearing and raising of offspring, and her position in baboon society was subordinate to that of all males

ethology The study of the natural behavior of animals under natural conditions.

savanna The open grasslands of the tropics.

FIGURE 8.2
Baboons on the African savanna. Our early ancestors might have witnessed scenes like this.

and specifically determined by the position of the male with whom she mated.

Recent studies have shown, however, that baboon societies are far more complex and variable (Fedigan and Fedigan 1988; Smuts 1985, 1995; Strum 1987). While male baboons do vie for dominance, achieve differential social power and influence, and protect the group from other baboons and from predators—and while hamadryas males do maintain harems through violent coercion—a formal, permanent, tightly structured dominance hierarchy among males does not seem to be at the center of social organization in all cases. Among other types of baboons—for example, the olive baboons of equatorial Africa—social structure is based on "a network of social alliances" (Fedigan and Fedigan 1988:14), including friendships among females and between females and males. These

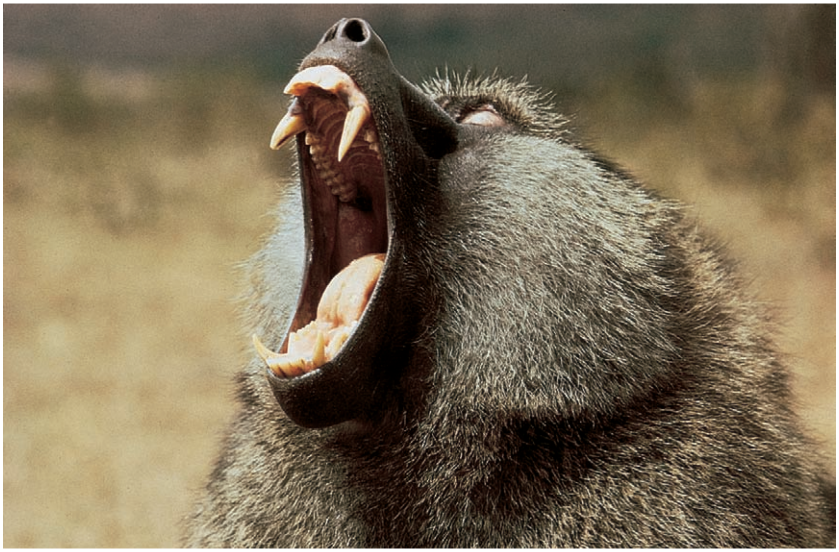


FIGURE 8.3
Baboon threat. A male baboon shows his long canine teeth and flashes his white eyelids in a "threat gesture," probably directed at a less dominant male.

friendships may be so strong that a male will aid his female friends' infants even though he may not be their father. Such friendships, rather than the social position of the males, may be what determines who mates with whom.

Differential social positions exist, but they are based not on those "masculine" traits mentioned previously but more on an individual's "experience, skill, and, . . . ability to manipulate others [and] mobilize allies" (Fedigan and Fedigan 1988:15). If there is any subgroup that is central to a troop and that ties generations together, it is that made up of related females; the males, being more mobile, are a less stable part of the troop than was previously supposed. In fact, the competition that may be most important to the troop is that among females, who compete with one another "over access to the resources necessary to sustain them and their offspring" (Fedigan and Fedigan 1988:5). Finally, it appears that mate choice is more a female prerogative. Males make overtures toward estrous females, but it is the females who decide with whom they will mate. Thus, females, by forming alliances with related females and by selecting the males with whom they will mate, are helping ensure their own reproductive and child-rearing success, as well as the success of their genes via the reproductive success of their close relatives.

The earlier interpretation of baboon social organization indicated that to survive on the savanna, the primates needed a tightly organized, male-oriented and dominated, almost militaristic society. The obvious conclusion was that the early hominid savanna dwellers probably had a similar set of behaviors and that our modern social systems are, to one extent or another, variations on this theme.

Again, however, we must remember that we share with baboons and other nonhominoids only the most general primate traits. Similarities between humans and baboons exist because we have evolved variations of the same basic primate behavioral themes. Our specific expressions of those themes, though, are the results of separate and independent evolutionary histories.

Nevertheless, those separate histories have produced results that are similar in baboons and humans and, as we shall see, in chimpanzees and bonobos: the adaptive focus of a social structure built around a family unit, friendships, mutual aid within the group, defense of the group, and recognition of individuals. This social structure at least tells us that such a focus is one possible adaptive path among primates, and so it is reasonable to assume that something like it was the key to the survival of the early hominids.

Chimpanzees

Some of the most remarkable results of ethological observations began with three landmark studies of the great apes: Jane Goodall's study of the chimpanzee, Dian Fossey's of the gorilla, and Biruté Galdikas's of the orangutan. Subsequent studies keep contributing to our understanding of these primates. Each study is interesting in its own right and tells us something of the possible variations on the basic primate pattern of social organization.

The orangutan (*Pongo pygmaeus*) is an Asian ape and is separated from us by 12 million years. The gorilla (*Gorilla gorilla*), while it exhibits many of the same basic social behaviors as the chimpanzee, is a rather specialized ape. Unlike the chimpanzee, it spends much of its time on the ground, and its almost exclusively vegetarian diet consists largely of ground plants. This species is not known to make or use tools. (Orangutans, however, have recently been observed using simple tools.) The species most relevant to our present subject are the chimpanzee and bonobo.

Much of what we know of the ethology of the chimp (*Pan troglodytes*) comes from over fifty years of research led by Jane Goodall (1971, 1986, 1990) at Gombe Stream National Park in Tanzania. Goodall's studies have shown that in addition to physical and physiological traits, we share with chimps a number of behavioral characteristics. These center on aspects of social interaction and are thus instructive for understanding our own behavior.

The bond between mother and infant is strong in chimps, as it is in most mammals. These apes, though, have large, complex brains, and infants have a lot to learn about their world before they can become functioning adults. Thus, the mother-infant bond is particularly long-lived and important, and the nature of that interaction can have a lasting effect on the rest of a chimp's life. Poor treatment by her mother, for example, often makes a chimp a poor mother herself when she bears young. Chimps have been seen helping their mothers with younger siblings, and siblings often remain close into adulthood. Chimps, in other words, *raise* their young, and the family bonds that result may last a lifetime.

The chimps in a group are arranged in a dominance hierarchy. Males are generally dominant over females, but among females a loose hierarchy also exists. Males compete with one another in an attempt to achieve the highest position possible. The rewards are access to feeding places and to females. Social position, though attained in males through violent-looking but seldom injurious actions (Figure 8.4), is maintained via a series of expressions, gestures, and vocalizations. One of the most important interactions is grooming (see Figure 7.8), which maintains social cohesion and on occasion is a sign of dominance when a subordinate male grooms his superior. Other expressions of social interaction include kissing, hugging, bowing, extending the hand, making sexual gestures, grinning, and vocalizing, and we can freely use these terms because the meanings of these actions in chimp society seem to be just what they are in human societies.

A chimp society, however, is in no way some sort of dictatorship. Instead, it is marked by cooperation and mutual concern, which is seen mostly within the family unit of mother and offspring (because chimps are sexually promiscuous, a female may mate with a dozen males during estrus and so the biological father is unknown). Throughout their lives, members of this family unit will protect and care for each other, especially in times of illness and injury. Males have even been known to help brothers in their competition for dominance.

Care also extends outside the family unit. Offspring are important to the group as a whole, and adults will come to the aid or protection of a youngster threatened with harm, possibly risking their own welfare, even if the youngster is not necessarily theirs. Goodall once observed an adolescent male adopt an unrelated youngster who had been orphaned (1990:202).

Group membership is somewhat fluid. Chimps, for various reasons, will leave a group, and outsiders will occasionally enter it. Despite this

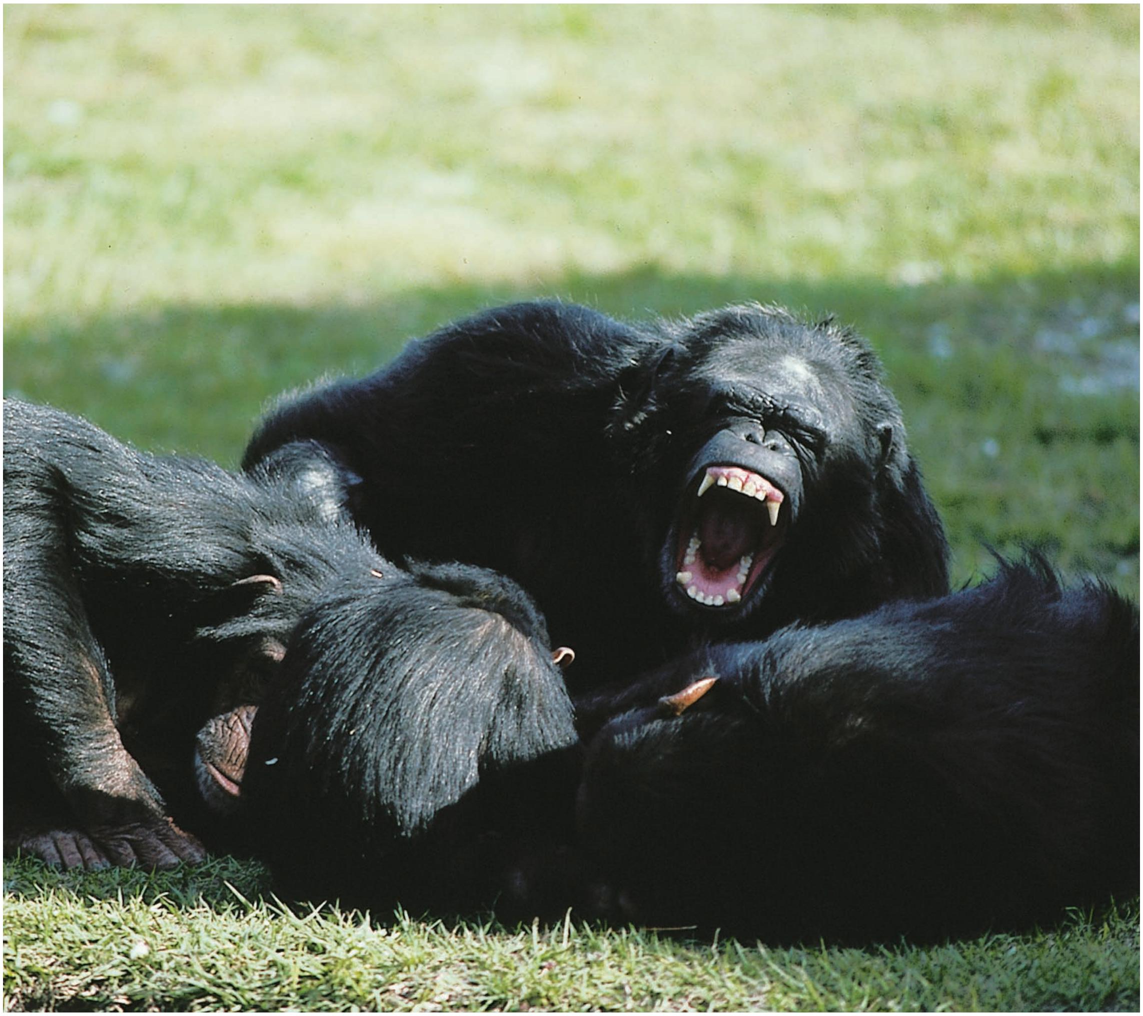


FIGURE 8.4
A male chimpanzee showing a “full open grin.” This expression is a sign of excitement, often used by a high-ranking chimp when in close contact with a subordinate. Compare this with the expression of the baboon in Figure 8.3.

fluidity, there is a sense of group identity and territory. Small bands of males will sometimes patrol the boundaries of their group’s range, and when they encounter members of other groups, they react to them as outsiders.

With chimps we may reasonably wonder about conscious motivation for some of these behaviors. In one chilling series of events, for example, males from Goodall’s main study group attacked and killed a female and all the males of a group that had broken away to establish

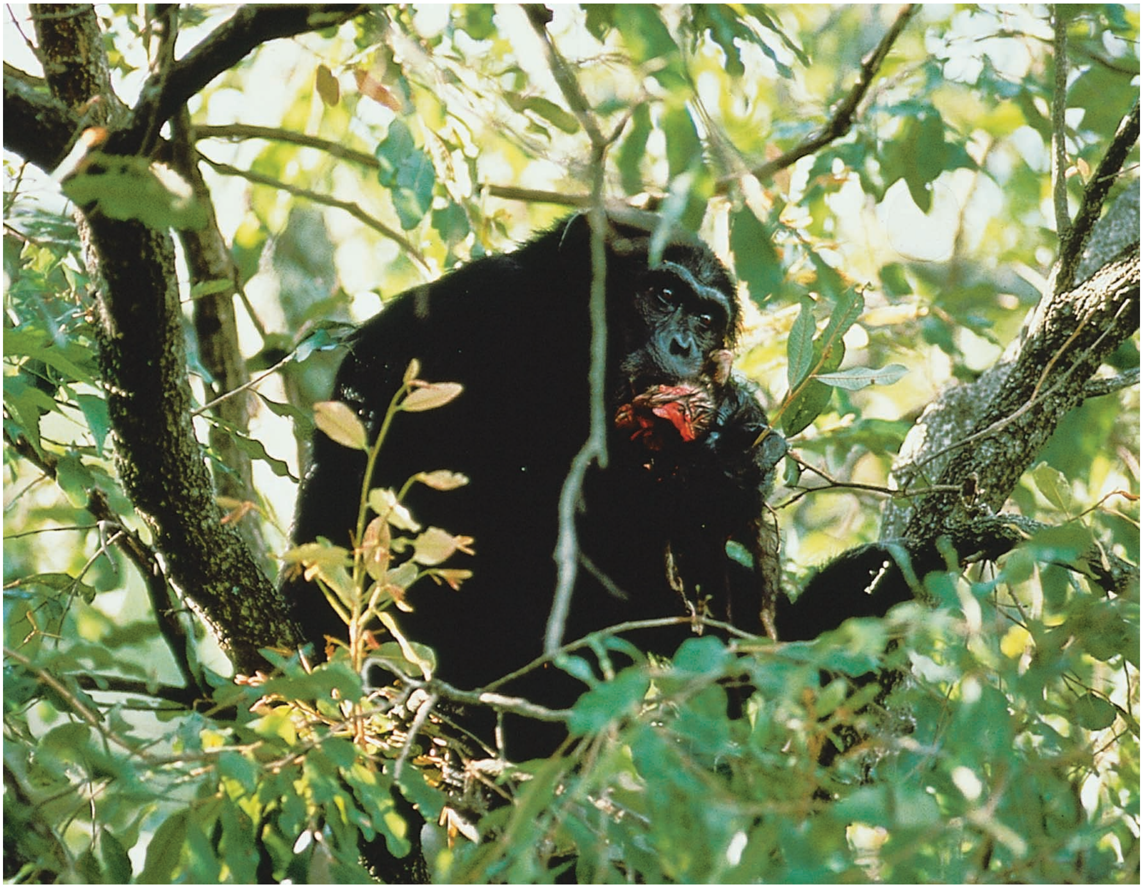


FIGURE 8.5
A chimp in Tanzania eats the carcass of a baboon he has recently hunted and killed. He may share some of his prize with close friends in his group.

their own territory. Goodall thinks the motivation may have been to reclaim the area. Although other examples of similar behavior have been reported, there is still debate over whether it is typical of the species. It has been suggested (Power 1991, for example) that because the researchers at Gombe interfered with the chimps' normal activities by providing food, they may have influenced the apes' behavior, including this event. Others (Sussman 1997) question how convincing the evidence is for similar occurrences.

Among the chimpanzee's wide range of food sources is meat. Chimps from some groups, including those studied by Goodall and associates at Gombe, are hunters (Stanford 1995, 1999). Males, and occasionally females, will hunt and kill small pigs, antelopes, and monkeys, including young baboons (Figure 8.5). The Gombe chimps, sometimes hunting in cooperative groups, kill over 100 red colobus monkeys a year, nearly a fifth of the members of that species within the chimps' range. Meat is the one food that chimps will share, and male chimps are more likely to share with friends than with rivals. There is evidence, too, that a male will hunt in order to get meat to give as an offering to a female in estrus. And we mentioned earlier the new observations of chimps making spears with which to hunt small primates.

Bonobos

Even more intriguing information has come to light about the third species of African ape, the bonobo (*Pan paniscus;* de Waal 1995; Ingmanson and Kano 1993; Kano 1990; Parker 2007; White 1996). The bonobo lives in the lowland forests of the Democratic Republic of the Congo and has been estimated by genetic studies (see Chapter 9) to have been separate from the chimp for 1 million to 2 million years. The population size of the bonobo is unknown and information about them comes in slowly. Because they live in remote areas and there is often political unrest in that country, much data on this species comes from captive animals.

Bonobos are sometimes referred to as *pygmy chimpanzees*. But bonobos are not pygmies at all; they are as large as chimps, though more slender and with smaller heads and shoulders. They have been said to walk upright more often than chimps but this does not appear to be the case (Figure 8.6). Like chimps, bonobos do some hunting (though less frequently) but show no evidence of cooperative hunting; further, females are sometimes the hunters. Also like chimps (see Figure 7.17), bonobos use tools, but never to acquire food. Rather, the bonobos use leaves as rain hats and drag branches to serve the social purposes of initiating and indicating the direction of group movement (Ingmanson 1996).

Bonobos are also said to be more peaceful and gregarious than chimps. There is a dominance hierarchy among males, but unlike the case with chimpanzees, the hierarchy is easily established with brief aggressive chases. Female hierarchies appear to be based on seniority. Also unlike chimps, female bonobos may dominate males (de Waal and Lanting 1997), and they hunt more regularly than do female chimps. All these depictions, however, have been questioned by the few studies done on bonobos in the wild (Parker 2007).

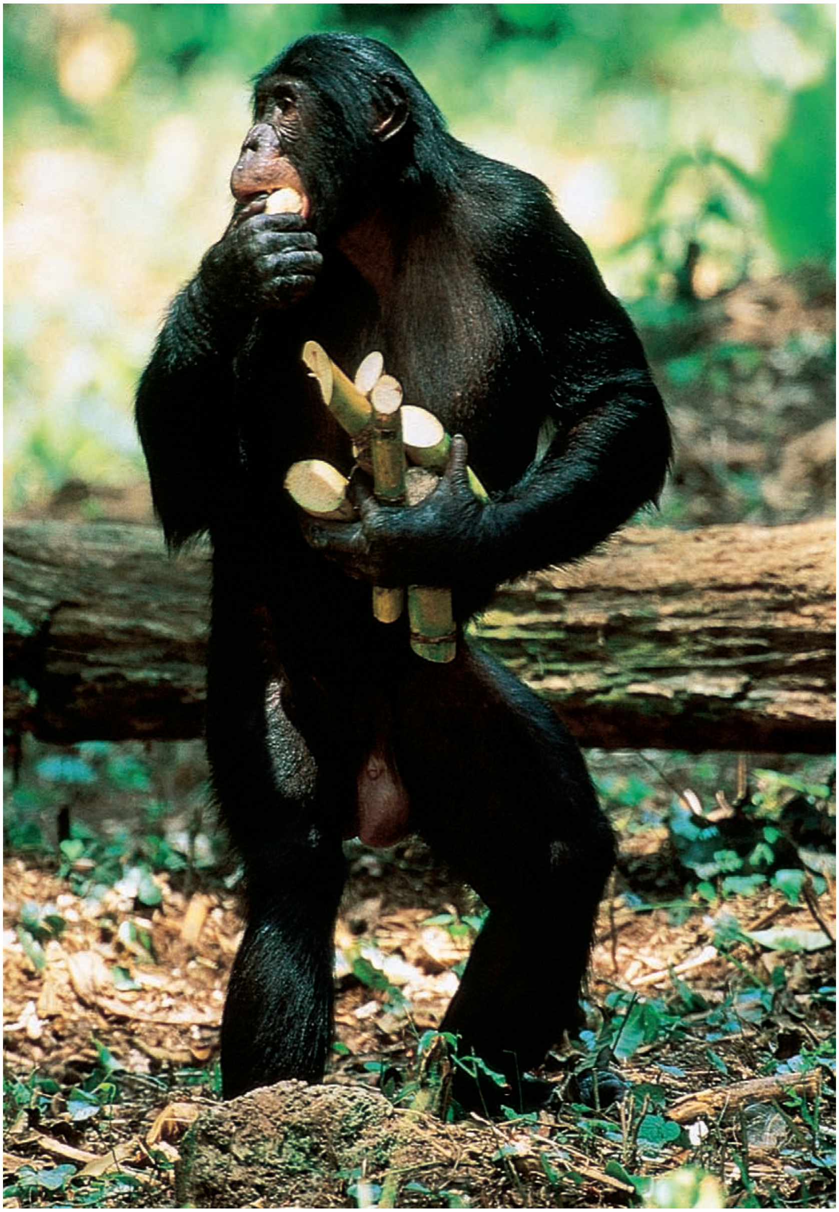


FIGURE 8.6
Bonobo standing bipedally. This bonobo is carrying stalks of sugarcane in his hands, now freed from locomotor activities. Note that he is walking bipedally because he is carrying food that has been provided to him by humans, an artificial situation.

Bonobos more readily share food with one another, and the food shared is not limited to luxury items such as meat (Figure 8.7). They have never positively been observed killing another of their kind, although violence does occur (Parker 2007), and their sexual behaviors contribute

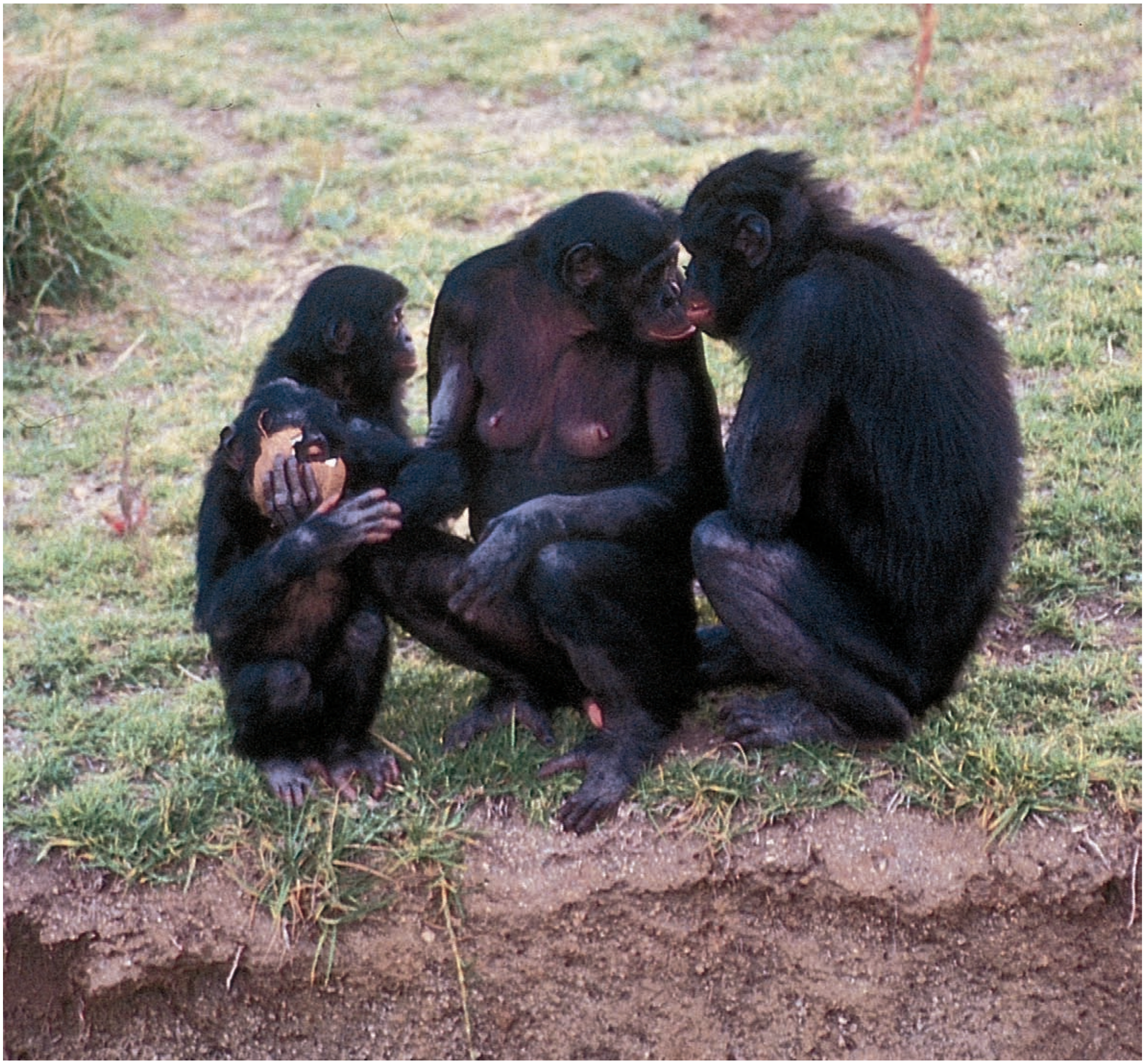


FIGURE 8.7
Bonobo society is characterized by peaceful relationships, with sexual activity and—as seen here on the left—food sharing as mechanisms to maintain harmony, ease tensions, reassure other members, and show reconciliation.

significantly to group cohesion. In contrast, sexual coercion, as seen in the hamadryas baboons, has been observed among the chimps of Gombe.

Bonobos, especially when feeding, constantly posture toward one another, rubbing rumps or "presenting" themselves as if initiating sexual activity. When sex does follow, it is usually face-to-face, a behavior uncommon in other primates except humans. Sexual activity is not limited to opposite-sex partners. Females commonly rub genitalia with other females, and males will mount each other.

Moreover, the signs of fertility, the estrous signals, seem nearly always present in bonobo females. In both chimps and bonobos, the fertile and sexual period is marked by a swelling and coloration of the skin of the genital area, which stimulate sexual interest in males. In chimps, the swelling occurs only when the female has ovulated. In bonobos, however, there is some swelling almost all the time, and they seem almost constantly sexually receptive. Sexual activity in this species has taken on a meaning separate from purely reproductive function. The motivation for sex may be as much psychological and social as it is instinctive

The function of this friendly posturing and sexual receptiveness seems to be the same as that of grooming and some expressions and gestures among chimps: to prevent violence, to ease tension (especially while feeding), to serve as a greeting, to signal reconciliation, or to reassure another group member. Sex or some form of sexual activity, between opposite- or same-sex partners, has even been seen to precede food sharing.

CULTURE AND SOCIAL COGNITION

The pioneering work of Goodall and others strongly indicated that humans' closest relatives have behaviors that are flexible, adaptable, and the result of intelligence and reasoning. More recent research substantiates these earlier findings. The following evidence shows that chimp and bonobo behavior, like human culture, varies from group to group.

For example, a chimp group in the forests on the west coast of Africa uses hammerstones to crack open nuts, something the Gombe chimps don't do, though the Gombe chimps are famous for their termite sticks (see Chapter 7). The West African chimps, in fact, use stone tools so regularly that they have left "archaeological sites" of the activity, made up of broken stones and nutshells (Mercader et al. 2002). These chimps also have different hunting techniques, relying more on cooperation between hunting males than do the Gombe chimps (Boesch and Boesch-Achermann 1991).

W. C. McGrew (1998) has suggested that this and other observations are evidence of cultural differences. A recent synthesis of data from seven well-established chimpanzee field sites across Africa, comprising an accumulated 151 years of observation, has shown variation in 571 different behavior patterns, not including those for which there are obvious ecological explanations (such as not nesting on the ground where leopards and lions are common). These patterns include tool use, grooming, and courtship behavior, and the nature of the variation points to the chimps' ability to invent new behaviors and pass them on socially—in which case

Contemporary Reflections

Are Some Human Behaviors Genetic?

Since Darwin's time, people have speculated about the possible biological bases of some human behaviors. Over the past forty years especially, a huge number of books have suggested biological bases for human aggression, social practices such as marriage patterns, altruistic acts, morality, territoriality, and many more. The more extreme versions of such ideas claim that we have a genetic program for such behaviors and that these programs evolved in the past and are maintained today because they confer a reproductive advantage on those who express them. In other words, they have been, and many continue to be, naturally selected for. According to opponents of this idea, a logical—and dangerous—implication of this claim is that variation in the specific expression of a behavior might reflect genetic variation among populations of our species.

Addressing this issue is complicated, but there are a few guiding concepts we may use to think about it. We must remember that genes are instructions for making proteins. It's a long way from the gene to the phenotypic trait, and the more complex the phenotypic trait, the longer the path and the more genes involved. Behaviors are *very* complex phenotypes. In short, just as there is no single "stature gene" that determines my height, there is no "aggression gene," or "marriage gene," or "altruism gene." Even in creatures with less complex nervous systems—ants, for example—whose behaviors *must* be biologically programmed, those behaviors are still complex responses of the whole organism to a whole host of environmental stimuli. There must be very many genes involved.

A behavior's biological program, then, is just a program for a potential or a general theme. Its expression requires some environmental stimulus (that is, something outside the genes themselves) and will vary as the exact nature of the stimulus varies. A biological basis for a human behavior can only be for

the behaviors might be thought of as "customs" (Cohen 2007; Whiten and Boesch 2001; Whiten et al. 1999). Similar data for orangutans has been described, although on a less complex level than that of the chimpanzees (van Schaik et al. 2003.)

Even more recently, sophisticated experiments using chimps have proposed such complex behaviors and cognitive abilities as the capacity for delayed gratification (Balter 2008); social cooperation that varies in degree according to the strength of social relationships (Miller 2007); and the ability to infer goals and motivations of others (Wood et al. 2007).

Finally, we should mention Kanzi, a male bonobo at the Language Research Center at Georgia State University (Savage-Rumbaugh and Lewin 1994a, 1994b). Kanzi is one of the most successful apes at communicating through a system with the characteristics of human language. He uses symbols on a computer keyboard; he can even recognize and, using his computer, respond to a large number of spoken English words. In addition the most general potential. Our cultural environment, which pervades every aspect of our individual and social lives, is immensely complex, and so the expressions of a behavioral potential must be varied indeed. Thus, the variation in a human behavior from society to society (or even from individual to individual) is largely a result of different cultural environments—different systems of belief and knowledge that mark the variety of humans' ways of life.

Language is a perfect—and fairly uncontroversial—example. All normal humans come equipped with the ability to take in raw data—the speech of the people around them and the responses to their attempts to communicate—and turn them into a working knowledge of their native language. Think about it: you spoke your native language fluently before you ever were formally taught all the grammatical rules in school. And you did it by yourself, using some built-in "software" in your nervous system into which data were fed by your senses. The ability to learn language is biological and thus, at its base, genetic. The genetic basis for this ability was selected for during our evolution (see Chapter 11). Linguistic ability conferred a reproductive advantage on our ancestors.

However, *what* language you speak, how well you speak it, what words you know, what accent you have—these particulars are cultural. They vary from society to society and even within societies—not because of genetic differences among populations but because of variation in the cultural contexts of which they are a part.

Similarly, the social system, with its sexual consciousness, that we see in bonobos may represent a common behavioral theme that we humans have translated into various sets of learned cultural norms such as sexual ethics and marriage patterns. Nature has given us behavioral potentials, ultimately coded in our genes, that we inherited from our evolutionary ancestors and that evolved over the course of our species' history. Culture has given rise to our specific expressions of those behaviors. In this way, yes, some of our behaviors may be said to have a genetic basis—but only in this limited way.

to his linguistic skills, he has been taught to make and use simple stone tools. Although not resembling even the earliest known hominid stone tools (see Chapter 10), Kanzi's tools are, nonetheless, true artifacts and so may show us what the *very* earliest stone tools of our lineage might have looked like. Neither of these behaviors—using a humanlike language or stone tool*making*—is seen among wild bonobos, but they do give us an idea as to the cognitive potentials of these apes.

Now, if all the behaviors of the chimp and bonobo sound more than vaguely human, the reason is simple. We share certain general behavioral patterns because we inherited them from a common ancestor. To be sure, our evolutionary line and that of the chimps and bonobos have been going their separate ways for 5 to 6 million years, and even shared features have had the chance to become modified by all the processes of evolution—to be changed, eliminated, enhanced, and differently adapted to our species' different niches. Chimps and bonobos are not "living fossils" stuck in some 5-million-year-old rut while our ancestors continued to evolve. But because our common ancestor is relatively recent and there is striking similarity between the bodies and behaviors of apes and humans, we can argue that our shared behavioral themes are homologies.

This does *not* mean that humans have specific genes for friendship, food sharing, territoriality, or continual sexuality. These are complex behaviors, and humans and apes are complex species. It does, however, hint that, as with the chimps and bonobos, the focus of the human adaptation—what adapted our earliest hominid ancestors and what has been the adaptive theme of our line—is social interaction based on individual recognition, a strong bond centered around family relationships (generally mothers and their offspring), long-term friendships, sexual consciousness, mutual care within the group, and recognition of and defense of the group. It seems reasonable to assume that our hominid ancestors behaved in similar ways. As Jane Goodall says,

> The concept of early humans poking for insects with twigs and wiping themselves with leaves seems entirely sensible. The thought of those ancestors greeting and reassuring one another with kisses or embraces, cooperating in protecting their territory or in hunting, and sharing food with each other, is appealing. The idea of close affectionate ties within the Stone Age family, of brothers helping one another, of teenage sons hastening to the protection of their old mothers, and of teenage daughters minding the babies, for me brings the fossilized relics of their physical selves dramatically to life. (1990:207)

SUMMARY

As we noted in the previous chapter, one way to guide us as we look at our own species is to understand the context from which our species evolved. This approach works for behavior as well as for physical adaptations. The importance of a well-defined social organization is seen among one savanna primate, the baboon, and is a good hint that an analogous behavior was a key to the survival of early savanna hominids.

More useful to understanding our own behavior is to examine the behavior of close evolutionary relatives, especially the chimpanzee and bonobo. Chimp and bonobo behaviors differ in specifics from ours and have been evolving separately from ours for 5 to 6 million years. All three species have adapted to different niches. The basic patterns for the behavior of all three species, however, are homologies. They are the same because we inherited them from a common ancestor. It is highly likely, then, that our remote hominid ancestors also manifested these patterns in some way.

Such studies indicate to us that the early hominids of Africa may very well have been highly social creatures and that their social organization was built around differing interpersonal relationships, a family unit, conscious sexuality, recognition of group membership and territory, and mutual care at both the individual and the group level.

QUESTIONS FOR FURTHER THOUGHT

1. Consider the debate over the biological basis of human behaviors. Much of the debate in both the scientific and popular presses has focused on such things as human aggression, intelligence, and sexual orientation. What are the ramifications of the extreme points of view (e.g., blank slate versus preprogrammed behaviors) of these topics? How might each be seen in terms of an intermediate model, as described in the chapter?
2. In fields as diverse as particle physics and cultural anthropology, it has been noted that the very act of scientific observation affects that which is being observed. Certainly this would also be the case for the ethological observation of nonhuman primates. What are the scientific as well as the ethical implications of this idea? Are some of our scientific ideas potentially inaccurate? Has studying other primates in the wild been in any way detrimental to them? beneficial to them?
3. If, as some authorities claim, apes exhibit behaviors that may be classified as cultural, how are we humans different in that regard? Is the difference in cultural behavior one of degree? Or is human culture different in kind? If so, how? While answering this question, keep in mind that although some nonhumans *have* culture, humans *are* cultural.

KEY TERMS

homology

ethology

savanna

SUGGESTED READINGS

Descriptions of baboon behavior can be found in Shirley Strum's *Almost Human* and in Barbara Smuts's *Sex and Friendship in Baboons*. Jane Goodall describes her work with the chimps and her experiences studying them in *Through a Window: My Thirty Years with the Chimpanzees of Gombe*. For a nice retrospective on Goodall's work see "Jane: 50 Years at Gombe" by David Quammen in the October 2010 *National Geographic*.

A good review of the biological basis of human behavior is Robert W. Sussman's *The Biological Basis of Human Behavior: A Critical Review*, second edition.

For more technical information on primate behavior, see *The Evolution of Primate Behavior*, by Alison Jolly; *Patterns of Primate Behavior*, by Claud A. Bramblett; *The Nonhuman Primates*, by Phyllis Dolhinow and Agustín Fuentes; and *Primates in Perspective*, by Christine Campbell et al.

Dian Fossey recounts her study of gorillas in *Gorillas in the Mist;* her own story, in turn, including her murder, is told by Farley Mowat in *Woman in the Mists* and in the 1988 movie *Gorillas in the Mist*. Biruté Galdikas tells about orangutans in *Reflections of Eden: My Years with the Orangutans of Borneo*.

Chimpanzee hunting behavior and the possible influence of meat eating on human evolution are the topic of Craig B. Stanford's *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. For a critique, see the review of Stanford's book "A Theory That's Hard to Digest," by Christophe Boesch in the 17 June 1999 issue of *Nature*.

For information on the cultural customs of chimpanzees, see "The Cultures of Chimpanzees," by Andrew Whiten and Christophe Boesch, in the January 2001 issue of *Scientific American;* "The Second Inheritance System of Chimpanzees and Humans," by Whiten, in the 1 September 2005 issue of *Nature;* and "Why We're Different: Probing the Gap Between Apes and Humans," by Michael Balter, in the 25 January 2008 *Science*; and "The Cultured Chimpanzees" by Gayathri Vaidyanathan in the 18 August 2011 *Nature*.

Bonobos are described in Frans de Waal's *Bonobo: The Forgotten Ape*, which has outstanding photographs by Frans Lanting. For more on the amazing Kanzi and other bonobos, see *Kanzi: The Ape at the Brink of the Human*

Mind, by Sue Savage-Rumbaugh and Roger Lewin, and *Apes, Language, and the Human Mind*, by Savage-Rumbaugh et al. A fascinating update on the bonobos is in the 30 July 2007 *New Yorker:* "Swingers," by Ian Parker.

An interesting Web site devoted to primate behavior is www.discoverchimpanzees.org.

9

CHAPTER

Studying the Human Past

> *The present contains nothing more than the past, and what is found in the effect was already in the cause.*
> *—Henri Bergson*

The study of the human past is a central part of biological anthropology. To understand the human species today, we need to know where, when, how, and from what we evolved. But the past *is* the past. We can't see past events as they were happening. We can't make them happen again. All we have are the present-day results of series of past events, such as the living species of primates we discussed in Chapters 7 and 8. In some cases we have the physical remains of the past—the fossils of extinct species—but these have themselves undergone change since they were part of a living creature.

The present, however, can be a powerful tool. Recall from Chapter 2 how Hooke and Steno used fossils and stratigraphy to plot the events of the past and how Hutton and Lyell used the idea of uniformitarianism by observing present-day processes to understand how past events took place.

In this chapter we will address the methods used by bioanthropologists to answer these questions about our past:

What are the features of the primate skeleton, and how can knowledge of them help us identify fossil remains?

How do we locate, recover, and date fossil remains?

How are fossils formed, and what affects the condition of the fossils we find?

What can we learn about our past from new technologies in the study of genetics?

BONES: THE PRIMATE SKELETON

Most of the physical remains we find of the evolutionary past are in the form of preserved bone. Only in rare cases are we lucky enough to discover soft-tissue remains of an ancient organism (see Chapter 14). Therefore, knowledge of skeletal structure, or **osteology,** is vital. The first thing we need to do, of course, is determine what species the skeletal remains are from. The human skeleton is a variation on the basic mammalian skeletal theme and, more specifically, on the primate skeletal theme. Figure 9.1 compares the skeletons of a modern human, a gorilla, and a domestic cat.

When we look at a skeleton, it's easy to imagine the bones as something separate from the muscles, nerves, blood vessels, and other soft tissues of the body. But, in fact, they all develop and function together. For example, the skull serves to protect the brain; therefore, a skull is a good indicator of the size and shape of the brain it once protected. Muscles are attached to bones, and so the location, size, and shape of the points where the muscles once attached to a bone will provide some indication of the size and shape of the muscles, even though the muscles themselves may have decayed long ago. We can tell a lot about a creature from the bones it leaves behind.

One of the more obvious and important things we can tell about a human skeleton is its sex. Humans belong to a species that exhibits **sexual dimorphism,** notable physical differences between the sexes that are not related to reproductive traits. In general, human males tend to be larger and more heavily muscled than females, a fact that also applies to the apes and to extinct hominid species. The skull and, for obvious reasons, the pelvis are the best features for identifying the sex of a skeleton (Figure 9.2).

Age at death may also be determined from skeletal remains. The body, including the bones, goes through many physical changes as it develops, matures, and ages, and many of these changes occur at fairly predictable rates. By determining on a skeleton which changes have already taken place and which have yet to take place, we may approximate the age at which the individual died (Figure 9.3).

The skeleton acts as a framework for the body, and thus the size and shape of the bones can reveal something of the appearance of the entire living person. We know, for example, from the sheer size and ruggedness of their bones, that a group of humans from ice-age Europe (the Neandertals, whom we will discuss in Chapter 11) were big, brawny, and extremely strong. Several investigators have attempted to reconstruct the faces of our ancestors from the shapes of skulls and facial bones. Using their knowledge

osteology The study of the skeleton.

sexual dimorphism Physical differences between the sexes of a species that are not related to reproductive features.

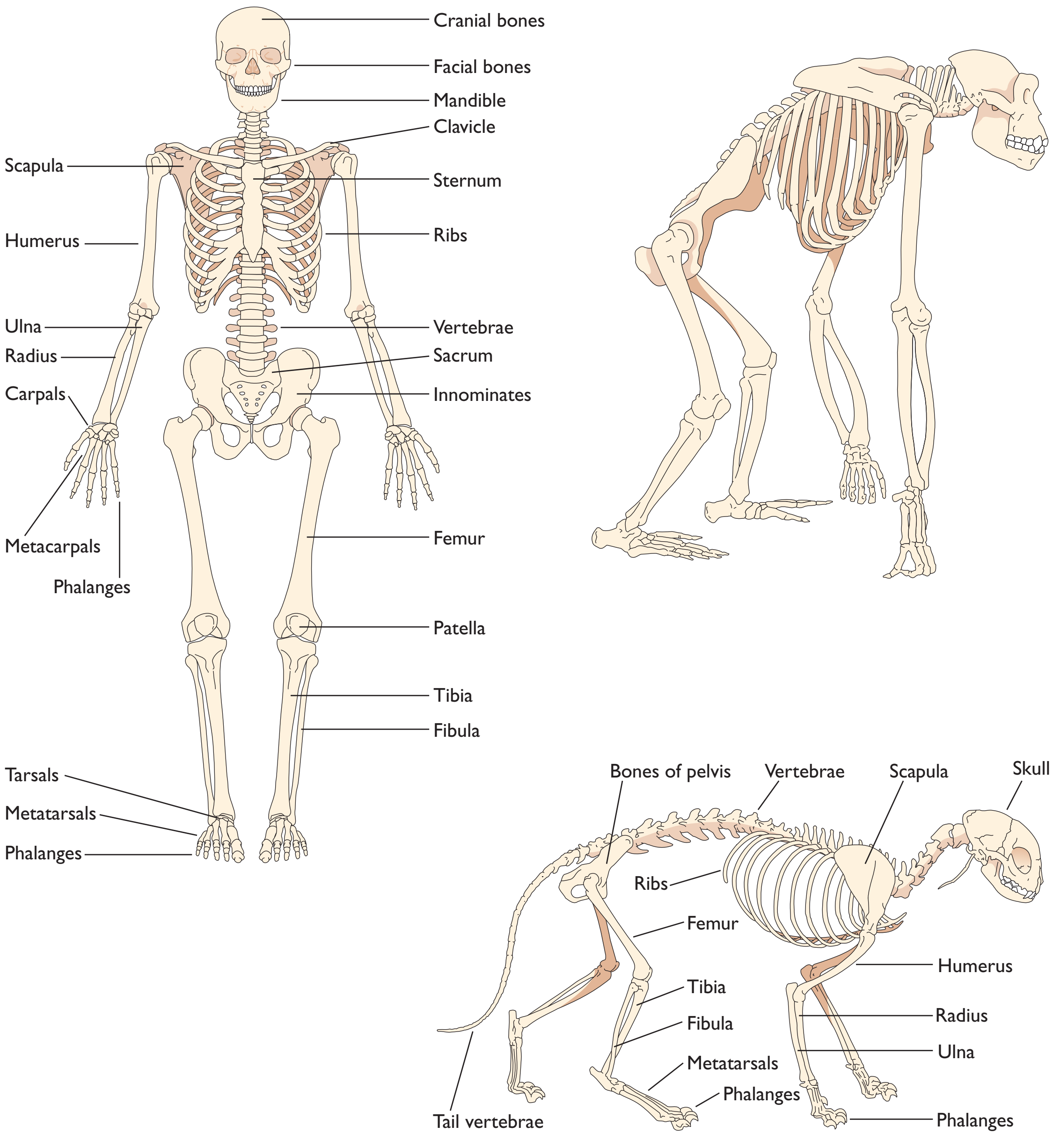

Cranial bones
Facial bones
Mandible
Clavicle
Scapula
Sternum
Humerus
Ribs
Ulna
Vertebrae
Radius
Sacrum
Carpals
Innominates
Metacarpals
Phalanges
Femur
Patella
Tibia
Fibula
Tarsals
Metatarsals
Phalanges
Bones of pelvis
Vertebrae
Scapula
Skull
Ribs
Femur
Humerus
Tibia
Radius
Fibula
Ulna
Metatarsals
Phalanges
Tail vertebrae
Phalanges

FIGURE 9.1
Skeletons of a modern human, a gorilla, and a domestic cat. (As a learning exercise, label the gorilla skeleton yourself.)

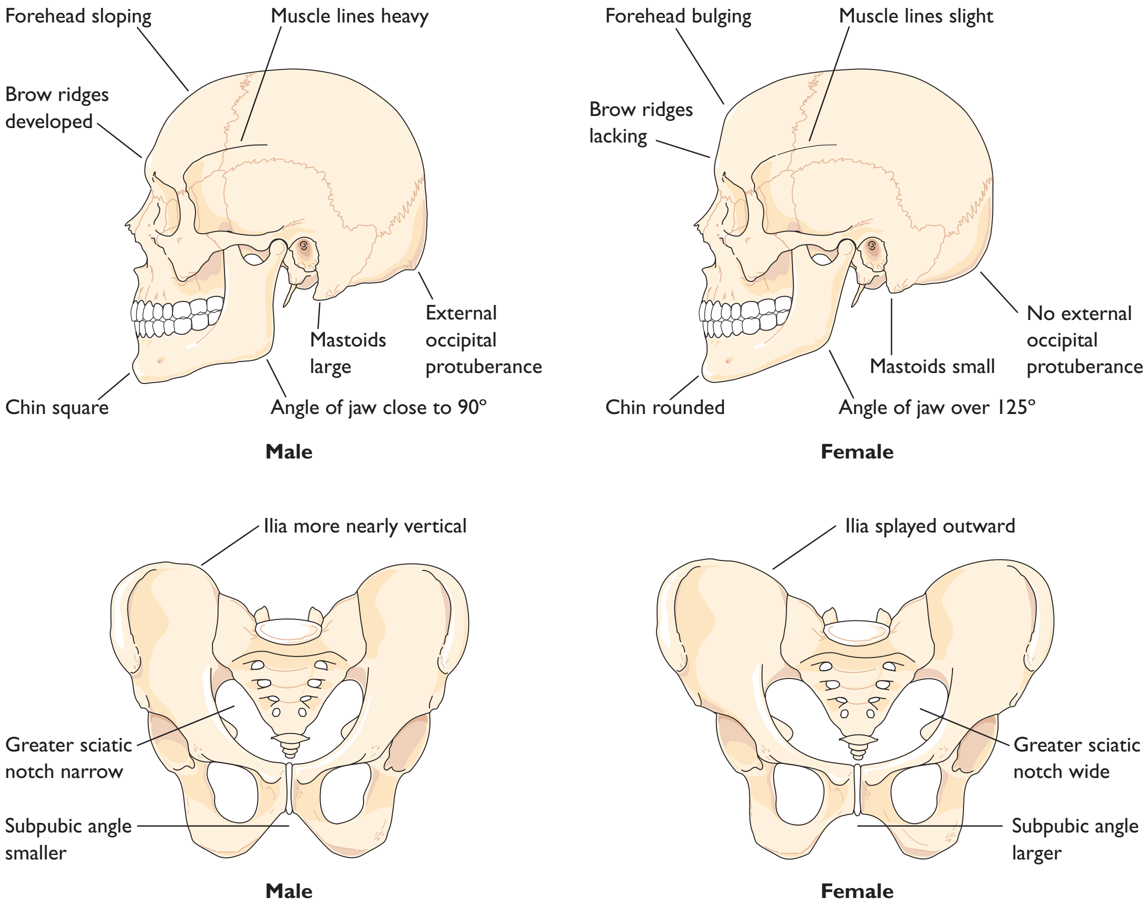
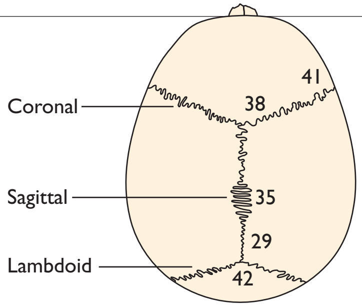

Forehead sloping
Muscle lines heavy
Brow ridges developed
External occipital protuberance
Mastoids large
Chin square
Angle of jaw close to 90°
Male
Forehead bulging
Muscle lines slight
Brow ridges lacking
No external occipital protuberance
Mastoids small
Chin rounded
Angle of jaw over 125°
Female
Ilia more nearly vertical
Greater sciatic notch narrow
Subpubic angle smaller
Male
Ilia splayed outward
Greater sciatic notch wide
Subpubic angle larger
Female

FIGURE 9.2
Major sex differences in the human skull and pelvis.

of human anatomy, they artistically add missing bones, eyes, fatty tissue, cartilage, muscle, and skin to casts of ancient skulls, "fleshing out" our picture of early humans (Figure 9.4; see also Figure 14.2). This technique is also used in law enforcement to try to identify skeletal remains. We will discuss the application of human osteology to legal matters in Chapter 14.

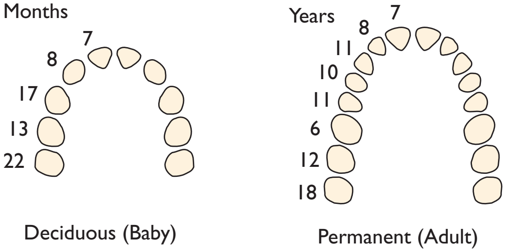
The skeleton can also tell us something about the behavior of the deceased organism. We have mentioned the importance of bipedal locomotion as the first hominid trait to evolve. We know it was first because the nature of the bones of the pelvis and femur, along with the position of the skull atop the spine, suggests posture and movement. Thus, our analysis of the bones of our most ancient ancestors provides clues as to how they walked (Figure 9.5; see also Chapter 10 for the evolution of this behavior).

Average ages for cranial suture closure (years)


41
Coronal
38
Sagittal
35
29
Lambdoid
42

Cranial Suture Closure. The bones of the cranial vault are separate at birth and gradually fuse during a person's lifetime. The numbers indicate the average age (in years) of complete closure at different points along the lines of attachment, the sutures. There are other dates as well, on locations not shown in this view. Because of the great degree of individual variation, this is not a particularly reliable technique, but it is still used.

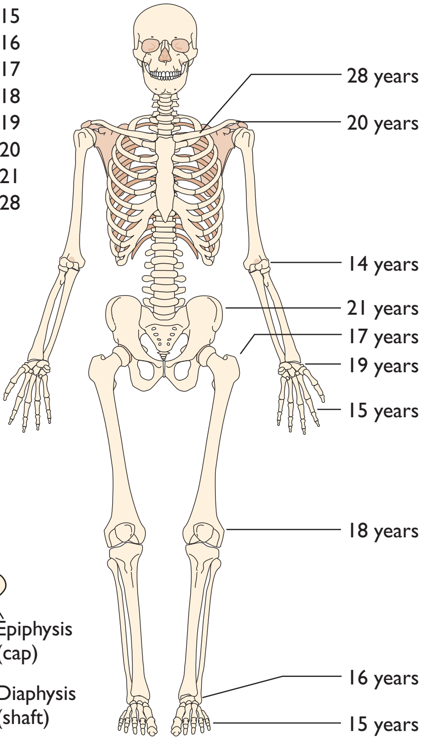
Eruption dates of deciduous and permanent teeth

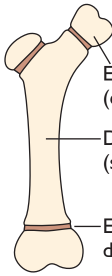

Months
7
8
17
13
22
Deciduous (Baby)
Years
7
8
11
10
11
6
12
18
Permanent (Adult)

Dental Eruption. Humans have two sets of teeth: deciduous, or "baby" teeth, and permanent, or adult teeth. Each tooth erupts through the gum line at a certain average age. We determine age by seeing which tooth was the last to erupt and which unerupted tooth would have erupted next. We recognize this method in our use of the term "six year molar" for the first adult tooth to erupt. The degree of development of each tooth below the gum line (seen in broken bone or in X-rays) can also be used.

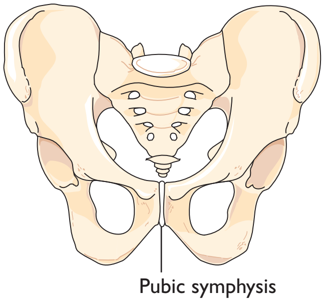
Ages of epiphyseal union (years)

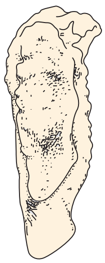
Elbow	14
Hand and foot	15
Ankle	16
Thigh (top)	17
Knee	18
Wrist	19
Shoulder	20
Hip	21
Clavicle	28


28 years
20 years
14 years
21 years
17 years
19 years
15 years
18 years
16 years
15 years


Epiphysis (cap)
Diaphysis (shaft)
Epiphyseal disk

Epiphyseal Union. The bones of the arms, legs, hands, feet, and other body parts grow in sections: a shaft, or diaphysis, and caps, or epiphyses. When growth is complete, the cartilaginous disks between caps and shaft turn to bone and a single bone results. Ages for epiphyseal union are uniform enough to provide a reliable aging method. The ages shown indicate that all the sites at any one location fuse at about the same time. For example, at the elbow, the far (distal) end of the humerus and the near (proximal) ends of the radius and ulna all fuse at approximately 14 years.


Pubic symphysis



Pubic Symphysis. The inner surface of the bones where the pelvis meets in front is called the pubic symphysis. Between the ages of 18 and 50+, the appearance of this surface undergoes characteristic changes. By assessing the phase to which a specimen belongs, we can approximate the age of a specimen at death. The symphyseal face shown is a Phase VIII, giving an age of 40 to 44 years. (Redrawn from Todd 1920.)

FIGURE 9.3 Major techniques used to determine the age of human bones.

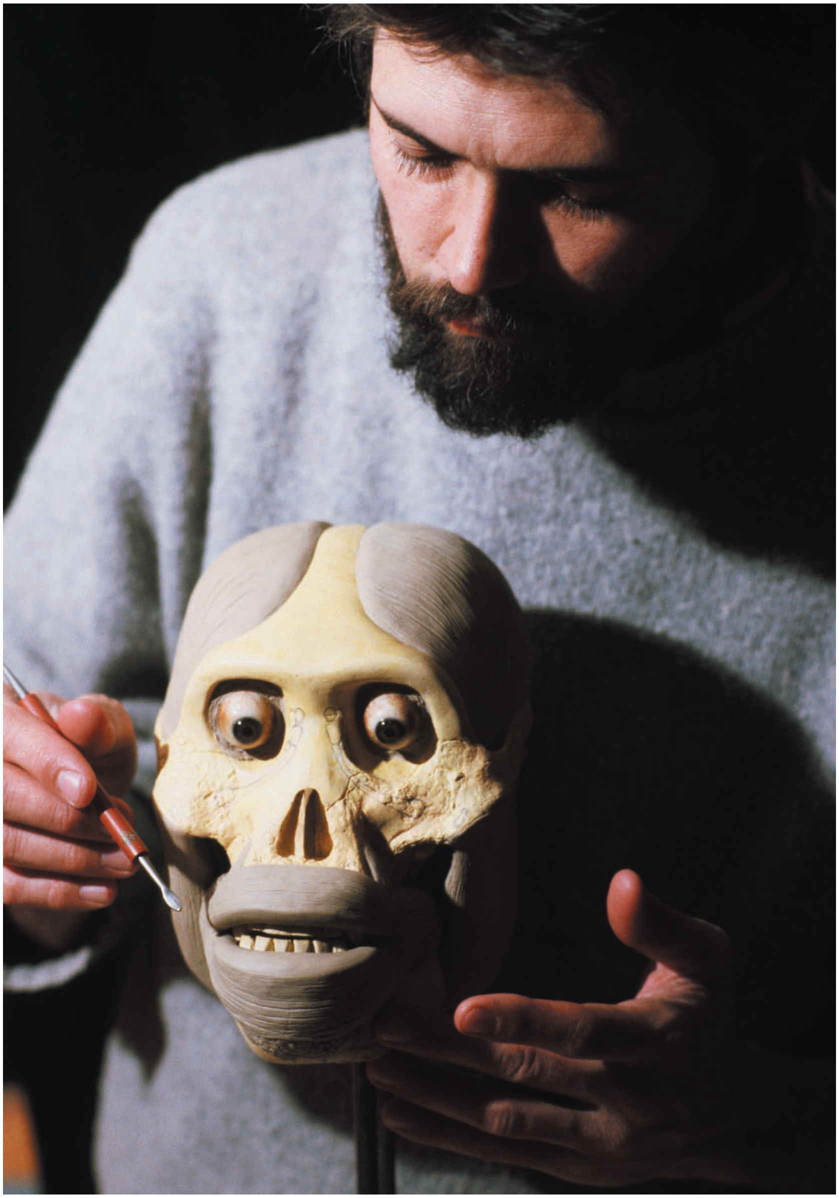


FIGURE 9.4
Using a cast of a fossil skull, an anthropologist adds modeling clay to flesh out the face of an ancient human ancestor.

carnivore An organism adapted to a diet of mostly meat.

omnivore An organism with a mixed diet of animal and vegetable foods.

Moreover, we can discern information about a deceased organism's diet from dental and skeletal remains. Look at the dentition of a **carnivore** in your dog or cat and compare it to the teeth of an **omnivore** in your own mouth. The teeth of the dog or cat, although they show some differentiation, are all pointed and sharp, adapted for grasping, piercing, cutting, and

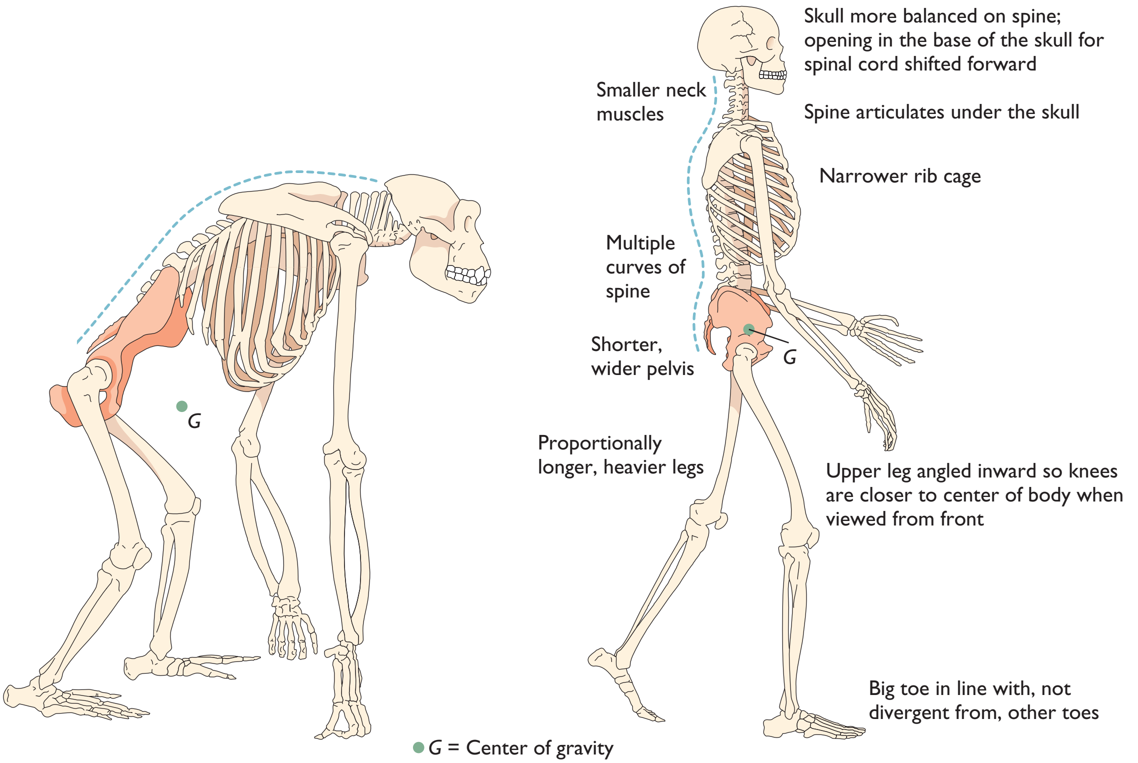

Skull more balanced on spine; opening in the base of the skull for spinal cord shifted forward
Smaller neck muscles
Spine articulates under the skull
Narrower rib cage
Multiple curves of spine
Shorter, wider pelvis
G
G
Proportionally longer, heavier legs
Upper leg angled inward so knees are closer to center of body when viewed from front
Big toe in line with, not divergent from, other toes
● G = Center of gravity

FIGURE 9.5
Note the anatomical changes and, thus, the physical evidence associated with bipedalism in the human primate. Compare human features with corresponding ones in the gorilla. *G* represents the center of gravity when standing bipedally. The ape expends much more energy to keep from falling forward when standing upright.

(Modified from John Napier, *The Antiquity of Human Walking,* © 1967 Scientific American. Drawing by Enid Kotschnigo)

crushing meat. Our teeth are adapted for a greater variety of operations and, thus, a greater variety of food types. In addition, certain wear patterns on the teeth, when examined microscopically, can reveal whether the organism's diet consisted of soft foods like fruits, or more abrasive, gritty foods like grains and roots. We can even examine the chemical content of ancient bones for the proportion of strontium, calcium, carbon isotopes, and other elements to determine whether plants or meat made up the bulk of the diet of certain populations.

Finally, we may acquire information about the health status of our ancestors, a field known as **paleopathology.** Many diseases leave characteristic marks on the skeleton. These include such important disorders as arthritis, tumors and other cancers, tuberculosis, leprosy, anemias, syphilis,

paleopathology The study of disease and nutritional deficiency in prehistoric populations, usually through the examination of skeletal material.

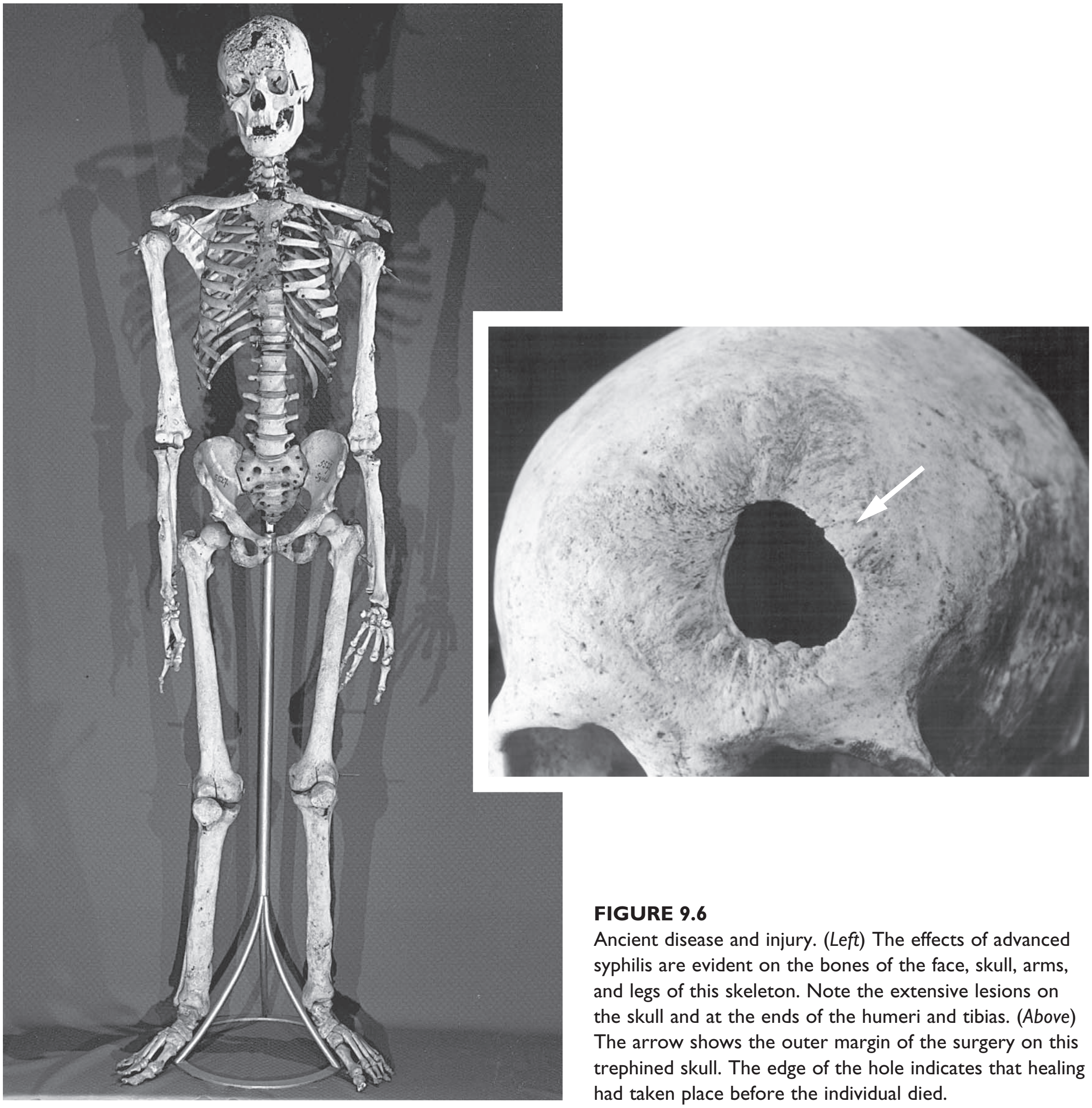


FIGURE 9.6
Ancient disease and injury. (*Left*) The effects of advanced syphilis are evident on the bones of the face, skull, arms, and legs of this skeleton. Note the extensive lesions on the skull and at the ends of the humeri and tibias. (*Above*) The arrow shows the outer margin of the surgery on this trephined skull. The edge of the hole indicates that healing had taken place before the individual died.

trephination Cutting a hole in the skull, presumably to treat some illness.

osteoporosis, and various infections. Injuries, too, leave their marks, as do other cultural behaviors, including scalping and **trephination,** a surgical procedure that involves cutting a hole in the skull, practiced even in prehistoric times (Figure 9.6).

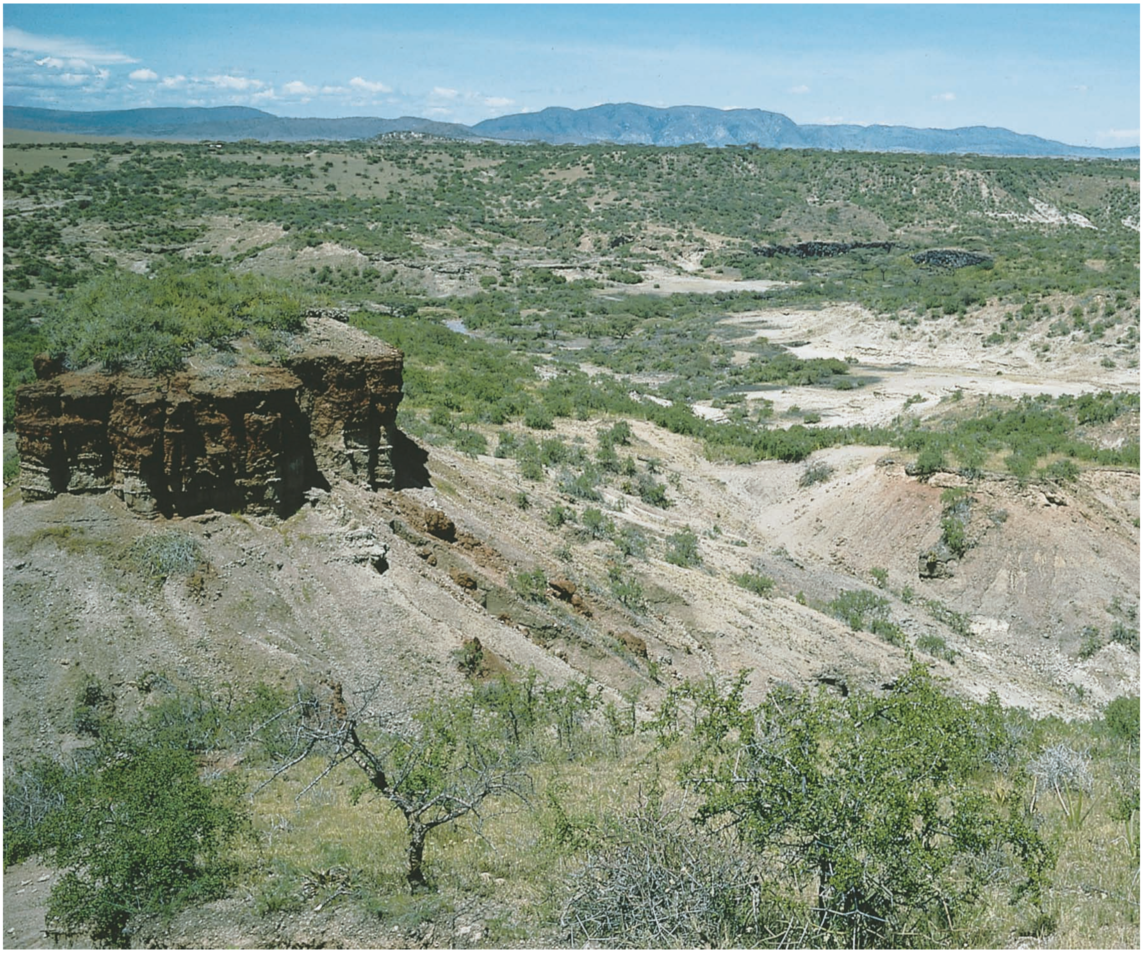


FIGURE 9.7
Olduvai Gorge, Tanzania. This location is one of the world's most productive sites for paleoanthropologists. The strata represent more than 2 million years of evolution.

OLD BONES: LOCATING, RECOVERING, AND DATING FOSSILS

Finding Fossils

Most creatures that have ever lived, including humans, have left no remains. Fossilization (which we'll discuss shortly) is a rare occurrence. A fossil, therefore, is really a priceless treasure, and finding one is an uncommon event—even in those **sites** that because of their geological history and nature yield many remains. Olduvai Gorge in Tanzania (Figure 9.7)

sites Locations that contain fossil and archaeological evidence of human presence.

has provided us with some of the most important hominid fossils, yet Louis and Mary Leakey lived and worked there for more than twenty years before finding one. How, then, do we even decide where to begin looking?

A lot, of course, depends on just *what* we're looking for. If it's dinosaurs we're interested in, we look in rock strata that date from the time of the dinosaurs. Anthropologists looking for hominid fossils need strata that were deposited in the past 5 to 6 million years.

It helps, too, if those strata are exposed by geological processes. Layers that are far under the surface might contain important fossils, but from a purely practical standpoint, it would be difficult, time-consuming, and expensive to dig them up. A place like Olduvai Gorge is ideal. There, an ancient river cut a canyon 300 feet into the earth, exposing layers of soil and rock that go back about 2 million years. At Omo, in Ethiopia, another important early hominid site, the strata have been tilted by geological forces, so that layers from 1 to 4 mya are all on the surface. Walking back and forth at such sites is like walking through time.

Recovering Fossils

Recovering fossils once they are located can be a tricky business. Fossils are old and often very fragile. Many old bones are **petrified**—turned to stone—and so can be hard to distinguish from the stone in which they were found (Figure 9.8). Raymond Dart, the discoverer of one of the most famous hominid fossils (both of whom we shall meet in the next chapter), took seventy-three days to separate the delicate fossil from the limestone in which it was encased (see Figure 10.10). The excavation tools of the paleoanthropologist, then, are not so much the backhoe or even the shovel but rather the mason's trowel, the dentist's pick, and the artist's brush.

A fossil sitting on a shelf in a lab or on display in a museum may be beautiful, intriguing, and provocative, but it is scientifically useless unless we know precisely where it was found, its **provenience.** To keep track of the proveniences of fossils, recovery is carried out with the utmost care directed at detailed and accurate record keeping. After all, a site is destroyed in the process of removing fossils, and we must have records of the relative locations of all the important items contained in that site.

Many early hominid fossils are simply found on the surface of the ground, exposed by wind and water erosion. Many, however, are dug out of the ground or are found associated with particular strata.

petrified Turned to stone.

provenience Here, the precise location where a fossil or artifact was found.

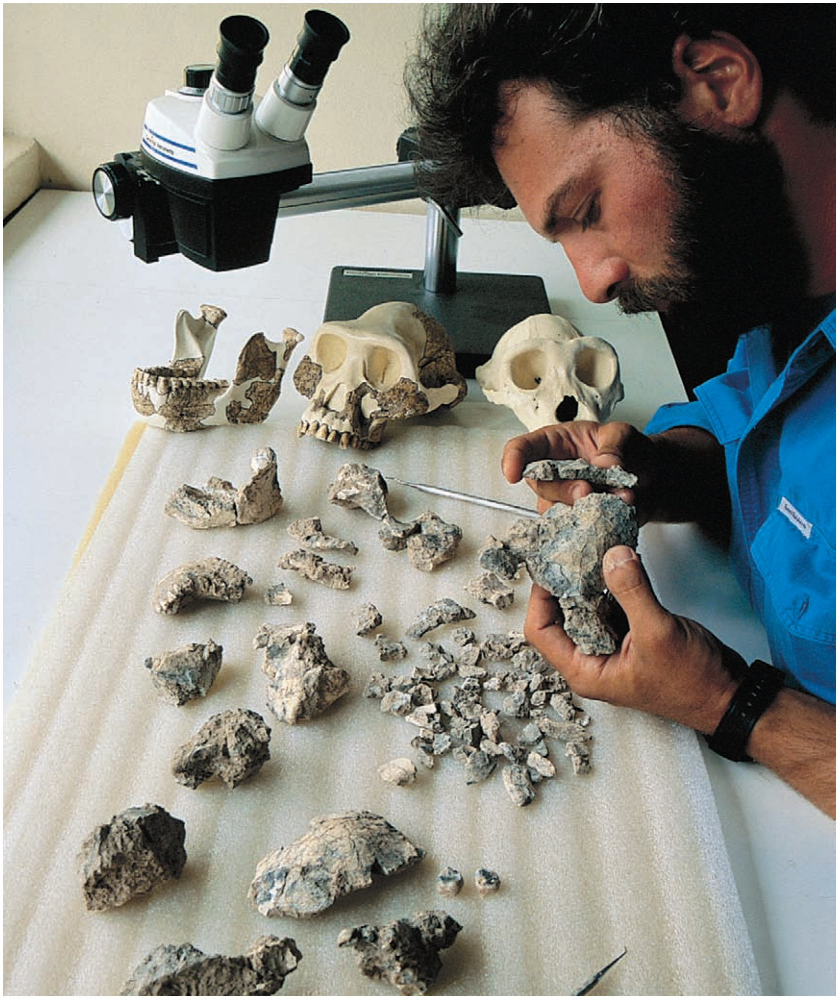


FIGURE 9.8
Paleoanthropologist Bill Kimbel of the Institute of Human Origins uses dental tools, a small drill, and a binocular microscope to chip stone from bone on nearly sixty fragments of a fossil hominid from Ethiopia. The results of his efforts are shown in Figure 10.12.

Dating Fossils

Relative Dating Techniques The depth at which a fossil is found in the natural strata of the soil or rock is, of course, an indication of its relative age. This is the principle of **superposition**—the deeper a layer is, the older it is. It is an important dating method and an example of a **relative dating technique;** that is, it indicates the age of one fossil in comparison with that of another (Figure 9.9). In the absence of any natural stratigraphy,

superposition The principle of stratigraphy that, barring disturbances, more recent layers are superimposed over older ones.

relative dating technique A dating method that indicates the age of one item in comparison to another.

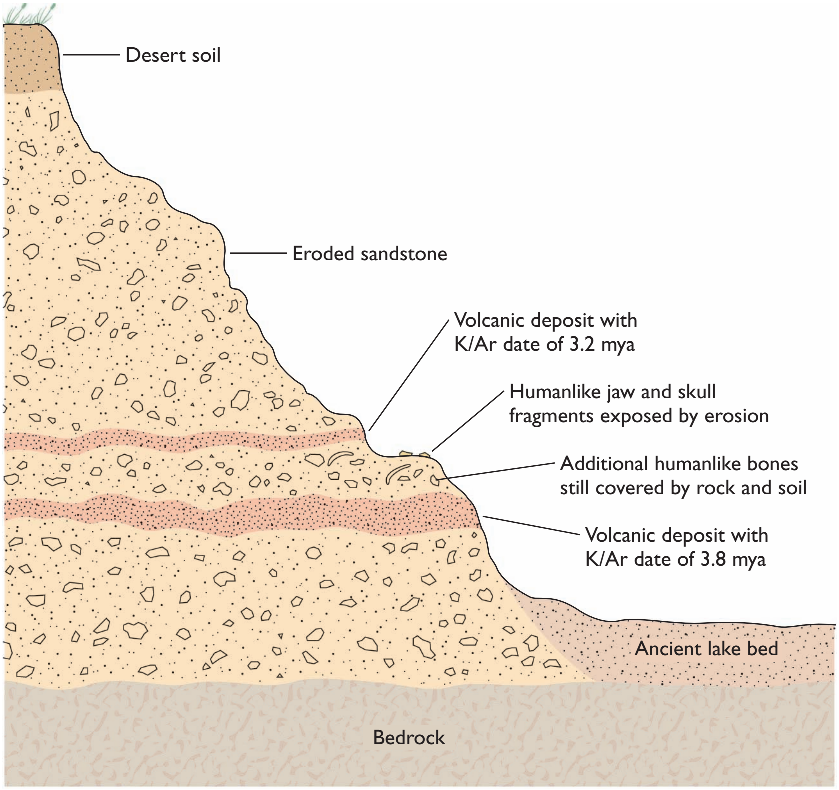

Desert soil
Eroded sandstone
Volcanic deposit with K/Ar date of 3.2 mya
Humanlike jaw and skull fragments exposed by erosion
Additional humanlike bones still covered by rock and soil
Volcanic deposit with K/Ar date of 3.8 mya
Ancient lake bed
Bedrock

FIGURE 9.9
Hypothetical stratigraphic sequence. The humanlike remains are between two layers of volcanic rock that can be dated using the K/Ar (potassium/argon) method. The remains must be younger than the volcanic deposit below and older than the one above.

the excavator of fossils must establish one. For example, the investigator may dig down by regular increments, perhaps only centimeters at a time, recording the precise depth of any item of interest.

Fossils can also be dated relative to their stratigraphic correlation with other fossils of known age. This is the principle of **biostratigraphy.** This dating method has been used in some of the early hominid sites in South Africa. Many of these sites are located in limestone caves, which are difficult to date by the techniques discussed in the following paragraphs. But when nonhominid fossils of known age are found in association with hominid fossils, we may infer the age of the hominids.

biostratigraphy The study of fossils in their stratigraphic context. Used as a relative dating technique.

Similarly, the horizontal location of each fossil is important. Often a paleoanthropologist—like the archaeologist looking for human cultural remains—uses a grid system. A site is divided into squares, or grids, and

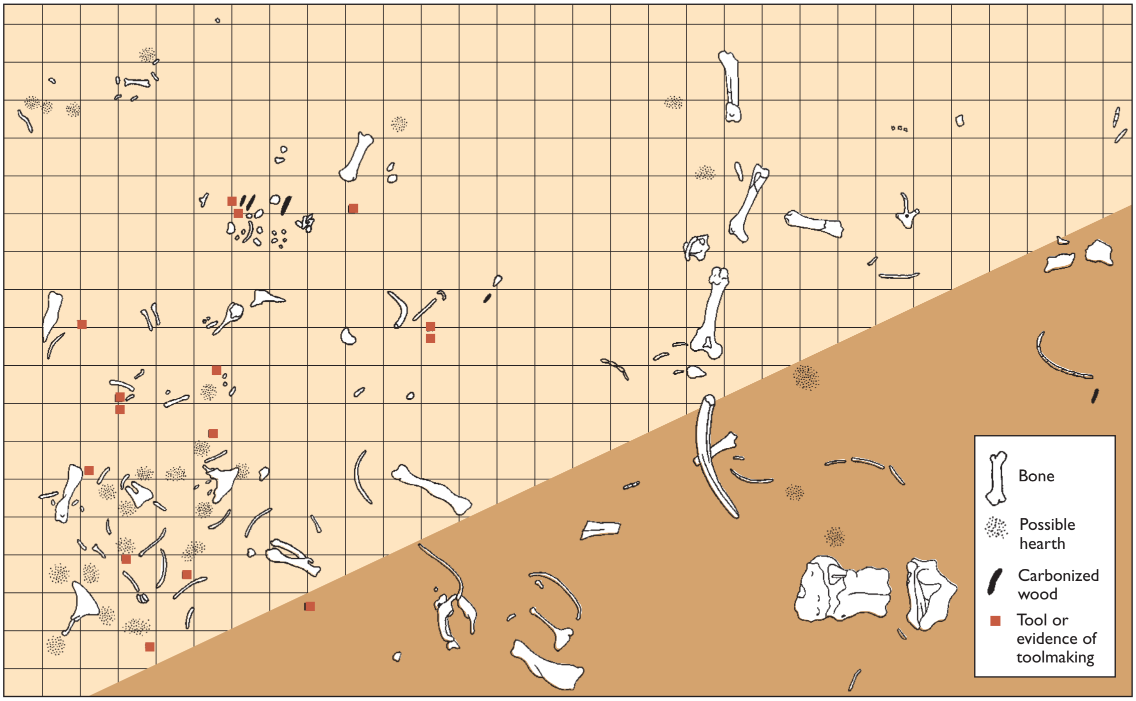


FIGURE 9.10
Grid system diagram from an excavation in Ambrona, Spain, dated at around 350,000 ya (see Chapter 11). The grid helps record the precise location of each bone and artifact. Notice how much less information is conveyed by the part of the drawing that does not show the grid.

each grid is excavated separately (Figure 9.10). The precise location of a fossil, relative to that of others at the same level, is recorded through photographs and maps.

Absolute Dating Techniques To determine the actual age of a fossil, we use **absolute dating techniques.** Among the best known are **radiometric** techniques. They all have essentially the same basic premise: if you know the rate at which some natural process occurs, and if you know how much of that process has already occurred, you can calculate the time at which the process started. There are several radiometric techniques, but two that are particularly useful in paleoanthropology will give you the idea.

absolute dating techniques Dating methods that give specific ages, years, or ranges of years for objects or sites.

radiometric Referring to the decay rate of a radioactive substance.

radiocarbon dating A radiometric dating technique using the decay rate of a radioactive form of carbon found in organic remains.

Perhaps the best known is **radiocarbon dating,** which can be used to date fossils back to about 50,000 ya and so is relevant to the later period of human evolution. It works as follows: Carbon is found in all living things, which continuously exchange it with the environment through respiration and metabolism. Nearly all carbon is ^{12}C, indicating that there are twelve particles in the nucleus (six protons and six neutrons). Some carbon, however, is called *carbon 14*, or ^{14}C, because it has two extra neutrons. Carbon 14 is continually being produced from nitrogen in the atmosphere by the impact of high-energy particles emanating from deep space that constantly bombard the earth. We know the proportion of each form (*isotope*) of carbon in a living organism. Once an organism dies, however, it no longer takes in new carbon, and so its ^{14}C—an unstable, or radioactive, isotope—begins to decay back into nitrogen, and it does this at a constant rate called a **half-life.** The half-life of ^{14}C is 5,730 years. In that time, one-half of the ^{14}C will have decayed. In another 5,730 years, half of the remaining half will decay, leaving a quarter of the original. And so on.

Now, if we find some organic remains—bone, for example, or even burnt wood from a campfire—we can test it to see how much ^{14}C is left compared to how much the organism contained when alive. We know how much ^{14}C a living organism should contain, and we test the amount left with a device that measures the amount of radiation emitted. Suppose that our specimen has one-quarter of the living amount of carbon 14. That means that two half-lives have passed, or 5,730 × 2, or 11,460 years.

half-life The time needed for one-half of a given amount of a radioactive substance to decay.

potassium/argon (K/Ar) dating A radiometric dating technique using the rate at which radioactive potassium, found in volcanic rock, decays into stable argon gas.

argon/argon dating A radiometric dating technique that uses the decay of radioactive argon into stable argon gas. Can be used to date smaller samples and volcanic rock with greater accuracy than K/Ar dating.

In fossils older than about 50,000 years, there is not enough ^{14}C left to accurately measure. So how do we date the really old fossils, like those of the early hominids? We could use another important method called **potassium/argon,** or **K/Ar, dating.** Radioactive potassium (^{40}K), decays into stable argon gas with a half-life of 1.31 billion years. Organic matter contains ^{40}K but loses the argon gas that it decays into. Volcanic rocks, formed during eruptions, trap the argon. Using the same reasoning as for radiocarbon dating, we test volcanic rock for the amount of argon, work backward, and date the eruption. Then, organic remains may be dated relatively: Any fossils found in a layer of volcanic rock are as old as that rock. Fossils found just above are younger; those found just below are older (see again Figure 9.9). Recently, a technique called **argon/argon dating,** which uses the decay of radioactive ^{40}Ar into argon gas (^{39}Ar), has proved more accurate in dating volcanic rock. With the use of lasers, it can be performed on a sample as small as a single crystal.

TABLE 9.1
Absolute Dating Techniques

Dating Method	*Age Range*	*Material Dated*	*Basis*
Accelerator mass spectrometry	70,000–100s BP*	Organic remains	Counts actual number of ^{14}C atoms
Amino (aspartic) acid racemization	1,000,000–2,000 BP	Bone	Measures shift in polarity of amino acids
Electron spin resonance	10 million–100s BP	Teeth, cave deposits	Measures electrons produced by natural radiation that become trapped in crystalline materials at a regular rate
Fission track dating	1,000,000–100,000 BP	Volcanic rock	Measures radioactive decay that leaves microscopic damage "tracks" in rock at a regular rate
Luminescence	To 800,000 BP	Fired clay, pottery, bricks, burnt rock	Measures amount of energy captured in material from the decay of radioactive elements in surrounding soil; amount of energy captured is proportional to age
Obsidian hydration	800,000 BP–present	Obsidian (volcanic glass)	Measures regular buildup of a "hydration layer," caused by the chemical reaction of obsidian to water over time
Paleomagnetism	2,000 BP–present	Material with magnetic minerals	Determines alignment of particles in natural deposits relative to the dated location of the earth's magnetic pole
Potassium/argon and argon/argon	billions–100,000 BP	Volcanic rock	Measures decay of radioactive potassium (or argon isotope) to stable argon gas
Radiocarbon	40,000–100s BP	Organic remains	Measures decay of radioactive carbon isotope to stable nitrogen
Uranium series	350,000–1,000 BP	Calcium carbonate	Measures decay of radioactive uranium to a series of other elements

*BP = "before present."

Other absolute dating techniques exist and are listed in Table 9.1, along with the preceding methods. Several techniques date volcanic rock; others can be used directly on organic remains. In many cases, more than one of these methods may be applied, and when they agree, we have a well-established date for a geological stratum or a fossil. Most of the dates presented in the following chapters are reasonably well confirmed through the use of one or more of these techniques.

HOW FOSSILS GET TO BE FOSSILS

Most animals and plants that have inhabited the earth have left no fossil remains. There may be whole taxonomic groups unknown to us because we've found no clues to their existence. Why is this so?

The conditions under which an organism, or some of its parts, can be preserved are quite specific. In New England, where I live, the soil is very acidic, due largely to the annual fall of leaves and pine needles. Organic remains tend to disappear very quickly. This is why we were surprised to find the intact skeleton of Henry Opukahaʻia (see Chapter 1). His bones were preserved because he was buried on a hill in sandy soil, so water, with all its related chemical and biological decaying activity, could not accumulate around him; additionally, the cemetery was probably regularly cleared of leaves.

Organic remains tend to be preserved under several conditions. In cases of extreme dryness, even soft tissues—usually eaten by everything from bacteria to insects to scavengers—may mummify. Natural mummies resulted from normal burials in the desert sands of ancient Egypt, even before the Egyptians began artificial mummification. In 1995, near the summit of the 20,760-foot volcano Nevando Ampato in Peru, the naturally mummified remains of a young Inca girl were found (Figure 9.11). Sacrificed to the gods of the mountains some 500 ya, her body was preserved by the cold and dry conditions of the high altitude (Reinhard 1996). (See Chapter 14 for another famous example—the "Ice Man" from the Alps.)

Lack of oxygen also contributes to preservation. Such conditions are found in the thick sediment at the bottom of some lakes and ponds. With no oxygen, there is little bacterial action, and organic remains decay very slowly. Many important fossils have been found in places that were once lake bottoms.

Of course, the longer ago an organism lived, the less likely we are to find its remains, simply because there is more chance that they will have been crushed, dissolved, eaten, washed away, and so on. But in rare cases minerals crystallizing out of water may form around slowly decaying soft tissue and fill in the spaces left by the decay. The fossils become petrified, literally turned to stone. The dinosaur fossils with which we are so familiar, as well as the remains of the earliest hominids are all stone. Luckily for us, the creatures that left these remains perished in just the right situations. Most creatures, however, aren't so considerate.

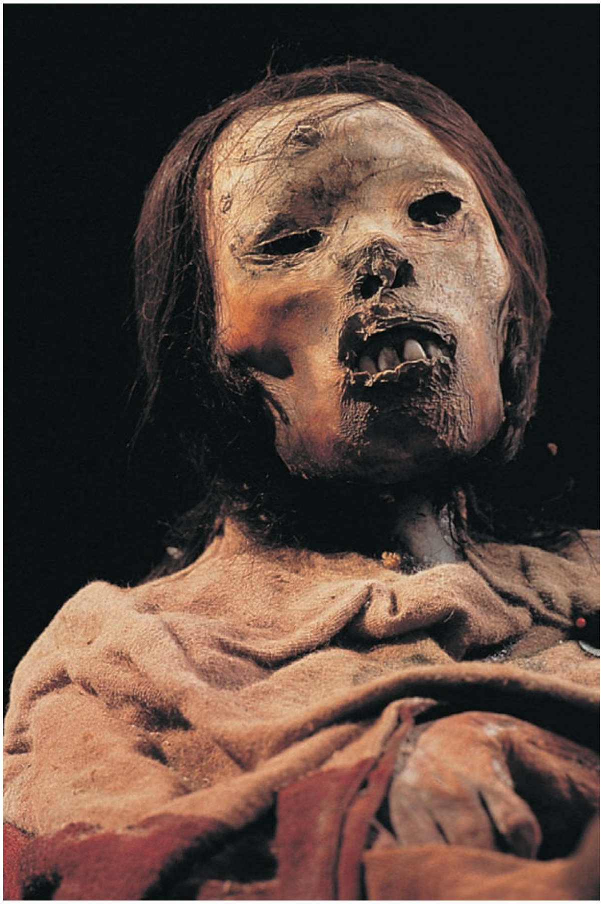


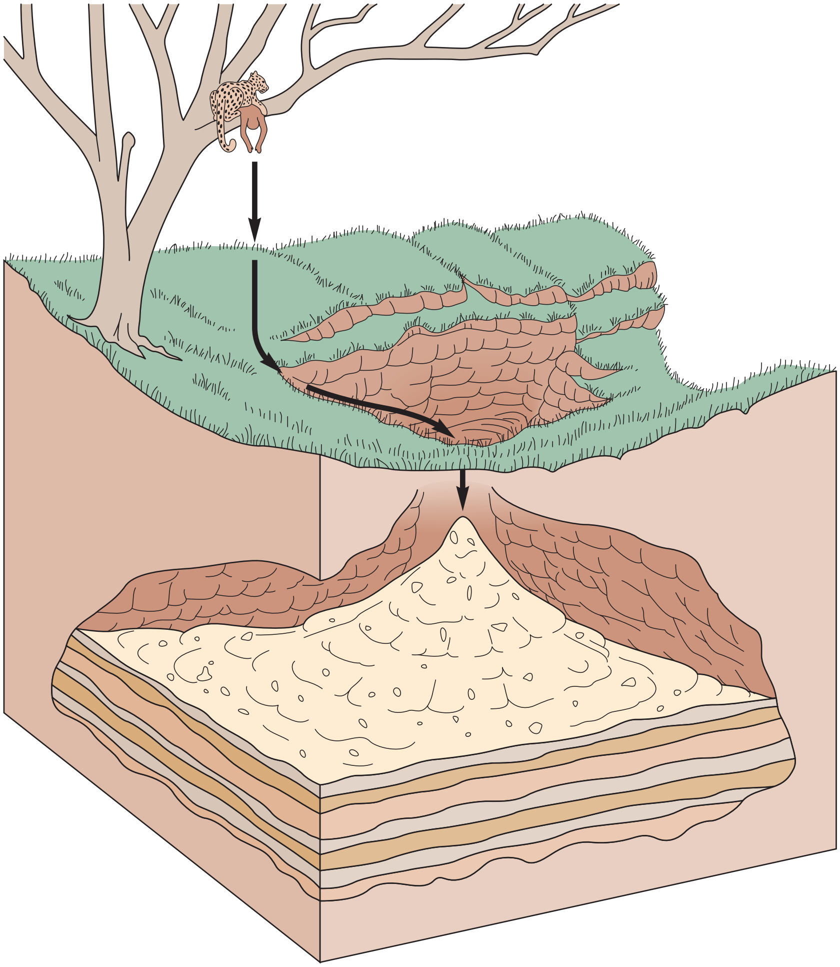
FIGURE 9.11
The Inca "Ice Maiden" is one of several naturally preserved mummies of sacrificial victims found in the Andes.

A fossil reveals more than just the type of organism it once belonged to. A fossil also contains clues as to how the animal died and what happened to it after its death. The study of these factors is called **taphonomy** (from the Greek word *taphos*, "dead"), and it has been important in our understanding of our own evolution.

taphonomy The study of how organisms become part of the paleontological record.

For example, some early hominid bones have been found in limestone caves in South Africa along with the bones of other mammals. These finds led investigators to believe that our early ancestors inhabited those caves and were hunters who brought their kills back home. More recent taphonomic analysis, however, reveals that the hominids were the hunted, not

FIGURE 9.12
This artist's reconstruction shows a leopard with the remains of an early hominid in a tree above the entrance to a cave. This scenario probably accounts for the accumulation of bones, including bones of our ancestors, in South African caves.



the hunters. The bones were the leftovers of leopard kills. Leopards often drag their prey up into a tree, where no other predator or scavenger can get at it. Although much of South Africa is dry, trees are able to grow around the mouths of limestone caves, which hold moisture. As leopard kills hanging in the trees fell apart—after being eaten over several days or decaying over time—the bones fell into the caves. Those bones were of antelopes, baboons, and other animals leopards eat. Apparently, our ancestors were on the menu as well (Figure 9.12). One early hominid skull shows twin puncture wounds that appear to have been the cause of death.

The lower canine teeth of a leopard fit exactly into these punctures, providing evidence for the preceding analysis. Although taphonomy is the study of the dead, it has told us important things about how our distant ancestors *lived*.

GENES: NEW WINDOWS TO THE PAST

The "Molecular Clock"

Just as we can reconstruct evolutionary relationships by comparing the anatomical traits of living creatures, we may do the same by making comparisons at the genetic level. In some ways, genetic comparisons are more accurate. Phenotypic traits are normally generated by a complex interaction of multiple genes, evolutionary processes, and environmental factors. As a result, a trait may look the same in two species, but the expressions of that trait in each species may be based on very different genetics.

On the other hand, two species may *look* very different, but their differences may be the result of extensive phenotypic effects of a very small number of genes, and the species may actually be quite close genetically. Humans and chimps are an example.

Comparing genetic differences among individuals, species, and higher taxa (genera, families, and so on) reveals actual biological relationships, no matter what the species look like or how seemingly similar or different some of their traits are. This work was pioneered, in the 1960s, by Vincent Sarich and Allan Wilson of the University of California at Berkeley.

It had been assumed prior to their work that humans and our closest relatives, the great apes, were separated by 12 to 15 million years of evolution. This estimate was based on the degree of phenotypic difference between us and them and on some 12-million-year-old fossils that *appeared* to show the beginnings of hominid traits. Wilson and Sarich's research showed that the blood proteins of humans and chimps are almost identical. In other words, our genes, at least for those traits, are almost the same. Comparing this difference with that between species whose evolutionary divergence time was known, Wilson and Sarich calculated that our two species had branched a mere 5 mya. These 12-million-year-old fossils, they concluded, were not hominids, no matter what they appeared to be. They were right, as we will see in Chapter 10. Other methods for

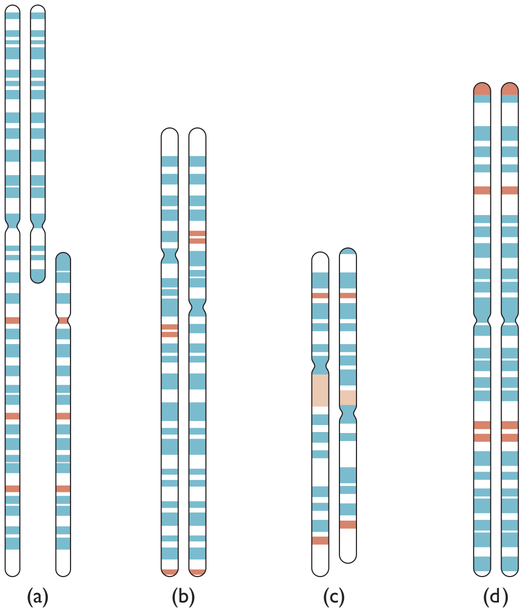


FIGURE 9.13

Comparison of human and chimpanzee chromosomes. Human chromosomes appear on the left in each pair and chimpanzee chromosomes on the right. The similarities in banding pattern (seen after applying a chemical stain) are clear. In pair (*a*) the pattern of human chromosome 2 is similar to that of two chimp chromosomes. In pair (*d*) the patterns are virtually identical. Banding patterns are the results of different concentrations of the four bases that make up the genetic code. Light bands are rich in noncoding sequences with mostly C's (cytosine) and G's (guanine; see Chapter 3). These tend to be associated with areas of high gene concentration. This is one type of early evidence for the genetic similarity between our two species.

making comparisons closer to the genetic level verified this hypothesis (Figure 9.13).

Today's technologies (see Chapter 3) allow us to look at and compare the most basic genetic components—the sequence of base pairs that make up the codons, which in turn make up the genes. We can now more precisely compare the genetic makeup of species, establishing just how genetically similar or different they are, and, using the logic described above, estimate how long ago their evolutionary lines diverged. This is one of the bases for determining the order of branching for the cladistic method, although recall the discussion of genetics versus phenotype and adaptation from Chapter 7.

The Genetic Differences between Chimps and Humans

A focus of recent studies, of course, is on the genetic comparison of humans with our closest relatives, the chimpanzees and bonobos. A well-known and well-accepted expression of this comparison says that humans and these apes are 98 percent genetically identical at the nucleotide level. While this does give a sense of the relative degree of our evolutionary closeness—which is no surprise anyway—it doesn't really tell us much. For one thing, since there are only four bases in the genetic code, any two long sequences of DNA from any two species are likely to be at least 25 percent identical (Marks 2002). Second, while some base sequences of human and chimp and bonobo DNA may be absolutely identical, they may show up in different numbers. For example, the base sequence of the gene for the Rh blood group is the same in humans and chimps, but humans have two such genes while chimps have three (Marks 2002:27). This phenomenon, called *copy number variation*, shows a 6.4 percent difference between our two species (Cohen 2007a). Finally, so-called *indels*, insertions or deletions of one to thousands of base pairs, and duplications of DNA sequences show about 3 percent difference between our species (Li and Saunders 2005). There's more going on than a simple numerical statement indicates.

Far more interesting and useful is to ask *which* genes differ between humans and chimps, *how* those genes differ, and *what* those genes do. There are some interesting possibilities. A chemical, for example, that all mammals, including the apes, possess on the surface of all body cells is lacking in humans. This is the result of some differences in a 92–base pair section of a single gene (Gibbons 1998b; Muchmore et al. 1998; Normile 2001). One function of this chemical is cellular communication during brain development and function, so a possible result of the genetic difference could be an influence on the timing and extent of brain growth. This has obvious implications for human evolution. Indeed, there is growing evidence for some major differences in brain structure between our species (Miller 2010).

Contemporary Reflections

Who Owns Old Bones?

In 1990 the nearly complete skeleton of a *Tyrannosaurus rex,* nicknamed "Sue," was found in South Dakota and soon became the center of a controversy over ownership. After some complex legal haggling, the owner of the land on which the bones were found was granted permission to sell them. The skeleton went up for public auction in October 1997 and was purchased (with corporate help) by the Field Museum of Natural History in Chicago—for $8.36 million! It will now be available for research and is currently on public display. In this case, everybody won, but scientists worry that this could set a precedent that would remove important evidence of the past from free scientific inquiry.

The issue of ownership and availability to science becomes even more complex when the remains of the past are human. In these cases, ownership may be a matter not only of landholding but also of direct biological or cultural descent. The extreme cases are easy enough to sort out. I don't think anyone would object to the excavation and study of early African hominids, even though they are the ancestors of us all. They are simply too far removed in time, and their potential scientific value is too great. On the other hand, I would object if some anthropologist wanted to dig up my grandparents, examine their bones, and put them in a museum case—and the law would clearly be on my side. Not all situations, however, are as clear-cut.

For years, well-meaning scientists have enjoyed the freedom to recover, study, and store the skeletal remains of the remote and not-so-remote ancestors of living peoples. In North America, thousands of Native American skeletons have been recovered—many of which were exhumed from the graves into which they had been placed by members of their societies. Although these remains have provided much information about the original inhabitants of this continent, Native American groups have voiced objections, for obvious reasons. In 1990 the Native American Graves Protection and Repatriation Act (NAGPRA) was passed. It says that lineal descendants have a right to the remains of their ancestors housed in institutions or discovered on federal or tribal territory. This legislation has led to the removal of large collections of human remains and associated artifacts from museums and labs and has made new excavations of Native American remains difficult, if not impossible. Indeed, before "naturally shed" remains were excluded

Another specific difference is in some genes for enzymes called *proteases*, which are important to the immune system (Check 2004). This could explain why chimps are less severely affected by some diseases such as AIDS and Alzheimer's.

A difference between nonhuman primates and humans has been located on a gene for a protein important in the building of some jaw muscles. Because of a mutation, the human version of the gene is inactivated, resulting in reduced muscle fibers and even a reduced size of some jaw muscles (Stedman et al. 2004). Moreover, the origin of this mutation from NAGPRA regulations, two local tribes demanded the return of some 10,000-year-old human hair found at a site in Montana, hair that could provide information on the DNA of early Americans (see Feder 1997 and references therein for a more complete discussion of this and related issues). A well-known example involves the skeletal remains discovered in 1996 in Washington State and commonly known as "Kennewick Man." A coalition of Native American tribes from the area laid claim to the 9,000-year-old bones under the terms of NAGPRA. Despite scientific testimony to the contrary, Secretary of the Interior Bruce Babbitt declared in September 2000 that the remains were culturally affiliated with the coalition and that the bones should be turned over to them. A suit by a group of scientists to gain access to the remains for study was reinstated. On February 4, 2004, a court of appeals ruled that the bones could be studied. As of this writing, the remains are at the University of Washington's Burke Museum, still legally owned by the Army Corps of Engineers, on whose land they were found.

Is there a compromise between honoring the cultural laws and heritage of indigenous peoples and providing science with important data—data that may even shed light on the history of the people in question? Each case, in the end, must be examined and judged on its own merits. Much evidence of early America is in the form of abandoned and naturally covered-over objects and bones, not intentional burials. Many of these remains cannot be reasonably affiliated with any specific living group and, thus, should be freely open to legitimate scientific investigation. Alternatively, scientists should not go into clearly identified burial areas armed with shovels and trowels. As is most often the case, where ancient bones are uncovered by natural processes or accident (say, during a construction project), the group with which those bones are affiliated might allow scientific information to be gathered before the bones are reburied. This is the situation with the well-known African Burial Ground in New York City. A model example for me is the case of Henry Opukahaʻia (see Chapter 1), where the family kindly allowed us to fully examine Henry's bones before preparing and returning them for burial.

Whatever the individual cases, however, there is one overriding consideration that should guide our actions—no matter how old or from what species, bones were once integral parts of living, breathing, feeling beings. Even when we can use them as scientific specimens, they deserve respectful treatment.

has been placed at about 2.4 mya, a date, as we shall see, that is about the time of the first fossils identified as belonging to our genus, *Homo*.

In addition to these specific differences, it has also been established that five chromosomes in our two species show significant differences in the arrangement of the same genes. Some sequences, for example, have been flipped in one species as compared to the other. These changes could lead to different roles for those genes. Identifying their functions is a current goal.

In the next two chapters we will outline the story of hominid evolution. All the above scientific techniques have been applied to studying this story and have allowed us to achieve what knowledge we have of our evolutionary history. As we will see, these new technologies have also been applied to comparisons among modern human populations (Chapter 13).

SUMMARY

Often when we read a brief article in the popular press about a new fossil find, we get the impression that the scientists conducted some sort of magic to arrive at their stated conclusions. In the 3 October 1994 issue of *Time*, for example, we read that a small fossil tooth and a few other fragmentary bones from Ethiopia had been discovered, heralding "a new chapter in the history of human evolution" (Lemonick 1994). On the basis of these bones, a new species of hominid was established. According to the scientists' description, the individual was probably bipedal, stood about 4 feet tall, was "ravaged by carnivores," and lived 4.4 mya in the forests. That's pretty specific information from a handful of bones turned to stone.

You should now understand that arriving at such conclusions is not magic at all. Although data like these bones are from a creature millions of years old, we may still use scientific methodology to interpret them. We know what modern mammalian skeletons look like and what previous fossil finds look like, so we can compare our new fossils with older ones in order to give them at least a provisional taxonomic assignment. As the fossils were being recovered in Ethiopia, scientists recorded exhaustive data about their provenience, allowing us to generate hypotheses about their environment and, using technologies from physics, when they lived. We understand how fossils are formed and what their specific condition can tell us about how the organism died and became part of the fossil record. We know, for example, what bones that have been "ravaged by carnivores" look like.

Finally, combining the preceding techniques with new methods from genetics, we have been able to piece together a tentative family tree of the hominids and related primates. When a new set of fossils is found, we have a context for comparison and a taxonomic system that can supply it with a name. We will meet this 4.4-million-year-old fossil species and many others in the next chapter, as we see exactly how these fact-finding techniques are applied.

QUESTIONS FOR FURTHER THOUGHT

1. Recently the Parliament of Iceland gave a private company the right to create and maintain a database on the health records, genealogies, and DNA profiles of nearly all living and many deceased Icelanders. The intent is to better understand links between diseases and genes. But there are privacy issues and concerns that the company may sell its information to pharmaceutical and insurance companies. What issues must be taken into account so that we might benefit from such a study while still respecting the rights of individuals?
2. Read about Kennewick Man on the Web site listed in this chapter's "Suggested Readings." What do you think about the motives of the scientists who want to use the remains for study, as opposed to those of the Native Americans who want to rebury the bones with no further study? Is a compromise possible? How should we approach remains that have definite cultural affiliations but that might hold important scientific information? How far back into history must we go to find human or archaeological remains that preclude such controversy?
3. Given the phenotypic, behavioral, and, especially, genetic closeness of our species to the chimps and bonobos, should we grant those species special ethical, moral, and even legal consideration? A committee of the Spanish parliament recently approved resolutions to protect apes from harmful experiments and to ban their use in circuses and TV commercials and films. Is this going too far for a nonhuman species? If not, what other nonhumans deserve such consideration? Where do we draw the line between those creatures that do and those that don't deserve such consideration?

KEY TERMS

osteology
sexual dimorphism
carnivore
omnivore
paleopathology
trephination

sites
petrified
provenience
superposition
relative dating technique
biostratigraphy
absolute dating techniques
radiometric
radiocarbon dating
half-life
potassium/argon (K/Ar) dating
argon/argon dating
taphonomy

SUGGESTED READINGS

A detailed and beautifully photographed book on the human skeleton, with life-sized pictures, is *Human Osteology*, second edition, by Tim White and Pieter Folkens. Analysis of the human skeleton in anthropological context is also covered nicely in *Human Osteology: A Laboratory and Field Manual of the Human Skeleton*, by William Bass; in *Skeleton Keys*, by Jeffrey H. Schwartz; and, for comparative osteology among the primates, in *An Introduction to Human Evolutionary Anatomy*, by Leslie Aiello and Christopher Dean. For a detailed treatment of anatomy and evolution that also includes considerations of soft tissue, see *The Human Strategy: An Evolutionary Perspective on Human Anatomy*, by John H. Langdon.

Techniques of excavation, interpretation, and dating are covered in more detail in Ken Feder and Michael Park's *Human Antiquity*, fifth edition, and in even more detail in *Field Methods in Archaeology* by Tom Hester, Harry Shafer, and Ken Feder.

Taphonomy is covered by Pat Shipman in *Life History of a Fossil: An Introduction to Taphonomy and Paleoecology* and by Lewis Binford in *Bones: Ancient Men and Modern Myths*.

More on the Ice Maiden and other mummies uncovered in the Andes can be found in three articles by Johan Reinhard in the June 1996, January 1997, and November 1999 issues of *National Geographic*.

The African Burial Ground is the topic of "Archaeology as Community Service: The African Burial Ground Project in New York City," by Warren Perry and Michael Blakey, in Kenneth Feder's *Lessons from the Past*. For the latest on Kennewick Man, see the following Web site: www.burkemuseum.org/kman

The Iceland genetics study is covered in "Decoding Iceland," by Michael Specter, in the 18 January 1999 *New Yorker*.

A thought-provoking book on the genetic similarities between humans and chimps, as well as other major issues in biological anthropology (including Kennewick Man), is Jonathan Marks's *What It Means to Be 98% Chimpanzee: Apes, People, and Their Genes*.

For more on the chimpanzee genome, see the series of articles in the 1 September 2005 issue of *Nature*, especially the lead article by the Chimpanzee Sequencing and Analysis Consortium. See also "Relative Differences: The Myth of 1%," by Jon Cohen, in the 29 June 2007 *Science*.

10 CHAPTER

Evolution of the Early Hominids

There are no final words. Human origins will always be enigmatic.
—Donald Johanson

Paleoanthropologists try to reconstruct the human past. The study of human evolution is a complicated venture. We have many thousands of individual pieces of data, each observed, measured, dated, and analyzed according to the very latest technologies. But when we try to put them all together, we come up with inconsistencies, contradictions, and often several equally plausible interpretations. This chapter and the one that follows will give you the most current ideas about our evolution, including all the missing pieces and alternative interpretations. We will address the following questions:

What is the evolutionary history of the primates?

When and under what circumstances did the hominids evolve, and why was bipedalism so important?

What is the fossil record of the early hominids?

THE ORIGIN AND EVOLUTION OF THE PRIMATES

The fossil record of the primates is spotty. Our identifications of most of the extinct primate species are based on fragmentary remains, mostly pieces of jaws or sometimes just teeth. Although a particular extinct species may be represented by many specimens, fossils of its contemporaries are often lacking, giving us little basis for comparison. There are large gaps in the primate fossil record. Some periods are represented by many fossils,

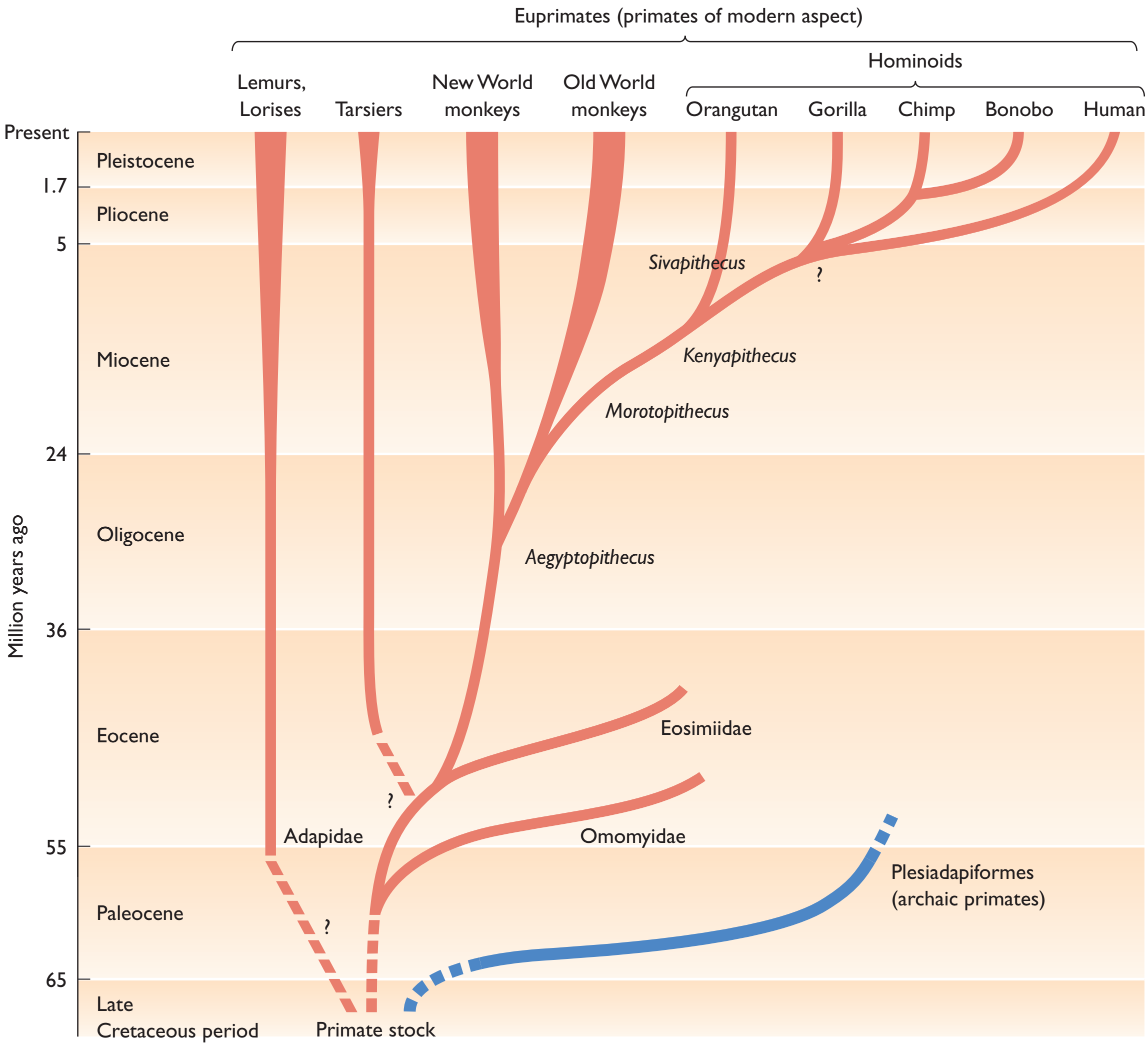

Euprimates (primates of modern aspect)
Hominoids
Lemurs, Lorises
Tarsiers
New World monkeys
Old World monkeys
Orangutan
Gorilla
Chimp
Bonobo
Human
Present
1.7
5
24
36
55
65
Million years ago
Pleistocene
Pliocene
Miocene
Oligocene
Eocene
Paleocene
Late Cretaceous period
Sivapithecus
?
Kenyapithecus
Morotopithecus
Aegyptopithecus
Eosimiidae
?
Adapidae
Omomyidae
?
Plesiadapiformes (archaic primates)
Primate stock

FIGURE 10.1
Simplified evolutionary tree for the primates, with major geological epochs and dates. Question marks and dashed lines indicate insufficient data to establish evolutionary relationships. This tree represents one of several possible interpretations.

but they all come from just a few sites. Still, we can put together a general, if tentative, picture of the course of primate evolution (Figure 10.1).

We have few fossils that tell us about the earliest stages of primate evolution. Some genetic comparisons point to the origin of the primates as far back as 80 to 90 mya, well into the time of the dinosaurs (Gibbons 1998a; Tavaré et al. 2002). In terms of hard evidence, there are a few primatelike teeth from Montana dated at 65 mya and some bones from Wyoming dated at 60 mya that have primate features related to climbing behavior. Remember that at the time, North America and Eurasia were still very close together and possibly still connected in some locations (see Figure 6.6), so the primates may have originated on the large northern landmass called Laurasia.

Undisputed primates appear about 55 mya. The traits that we associate in modern primates with an arboreal environment (see Chapter 7) probably first evolved to aid leaping as a means of locomotion in the forest canopy or the shrub-layer undergrowth and to promote fruit eating and "visually directed predation" on insects (Cartmill 1992). Modern mouse lemurs, lorises, and tarsiers all track insects by sight and seize them by hand. As the primates evolved, these basic traits proved a useful adaptive theme for life in the trees. Some fossil finds from Wyoming (Bloch and Boyer 2002; Sargis 2002)—representing an extinct branch of archaic primates (in blue in Figure 10.1)—clearly show features related to grasping, indicating that that adaptation evolved early in primate evolution.

The early primates come in three groups, all found in North America, Europe, Asia, and Africa. One group, the Adapidae, are thought to be ancestral to modern lemurs and lorises (Figure 10.2). Another group, the Omomyidae, date back as far as 60 mya and may be ancestral to both tarsiers and anthropoids (Figure 10.3). The Eosimiidae from Asia may represent direct ancestors of monkeys and hominoids. Important evolutionary shifts that marked the origin of the monkeys and apes included changes to (1) a diurnal lifestyle from a nocturnal one, (2) less leaping and more climbing through the trees with all fours, and (3) a more herbivorous diet with less emphasis on insects.

By 50 mya the Eastern and Western Hemispheres were completely separate. We know that all modern New World primates are monkeys, but there are very few monkey fossils from the New World, mostly because the jungle environment leads to quick and complete scavenging or decay of dead animals. Thus, we don't know for sure how the evolution of the primates proceeded in the Western Hemisphere. There are two views on the subject. The first is that the early New World prosimians moved into Central and South America when those areas joined together with North America and that the prosimians subsequently evolved into modern platyrrhines, the New World monkeys.

The second view is that early monkeys from the Old World "rafted" over to the Americas, unintentionally, of course, floating on logs and branches, "island-hopping" over a chain of volcanic islands when the two hemispheres were closer together. These early monkeys replaced any prosimians that still inhabited the New World, and they eventually evolved into the modern New World monkey species. Although there are some

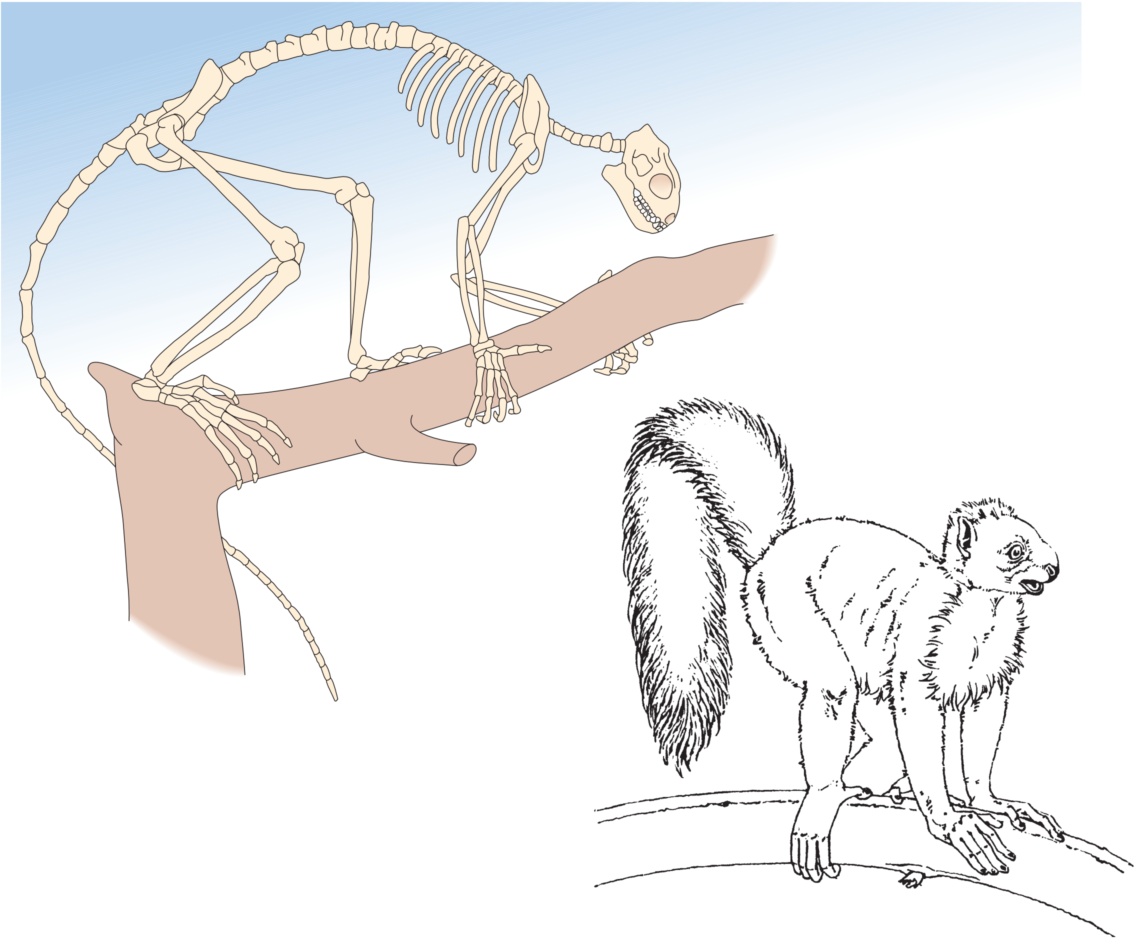


FIGURE 10.2
Skeleton and reconstruction of early adapid, *Smilodectes*. The form was similar to that of some modern prosimians. (Compare with Figure 7.11.)

distinct differences (see Chapter 7), the basic similarity between the Old World and New World monkeys argues for a single origin and thus for the second scenario. In addition, although most of the fossils from the New World are incomplete and therefore hard to evaluate, a find of a 25- to 27-million-year-old monkey from Bolivia (Takai et al. 2000), whose teeth are very similar to an older fossil form from Egypt, suggests that the New World monkeys originated and diversified first in Africa.

We are most interested in primate evolution in the Old World. From the site called the Fayum, near Cairo, Egypt, come a number of monkeylike forms dated from 40 to 25 mya. The most important, perhaps, is *Aegyptopithecus*, from about 34 mya (Figure 10.4). This 10-pound primate

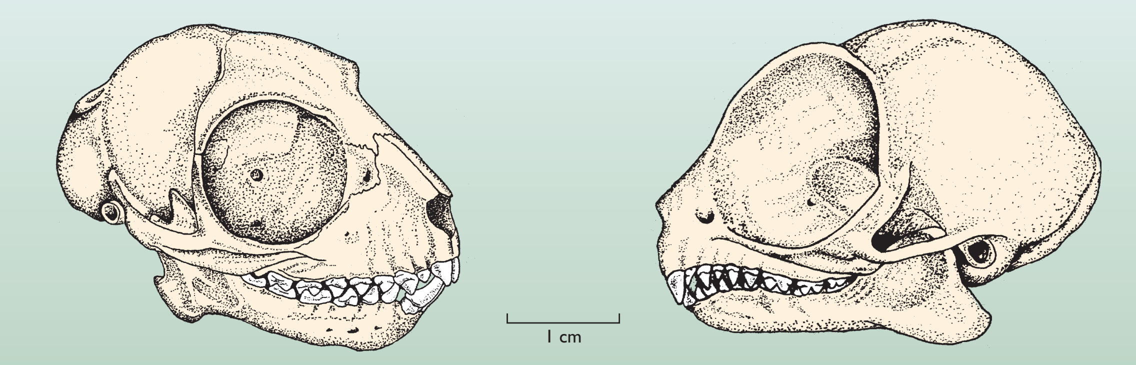


FIGURE 10.3
Fossil omomyid, *Necrolemur* (*left*), compared with modern tarsier. (See also Figure 7.12.)

shows anthropoid traits, as well as several features of the teeth, braincase, and skull that resemble later hominoids (apes and hominids). It could represent, then, the ancestor of all the modern Old World anthropoids.

As the early anthropoids expanded, they outcompeted the prosimians and pushed those more primitive primates into marginal areas. Most prosimians now live—as endangered species—on the island of Madagascar, which they probably reached by rafting, possibly aided by a land bridge. No other primates invaded Madagascar until humans got there.

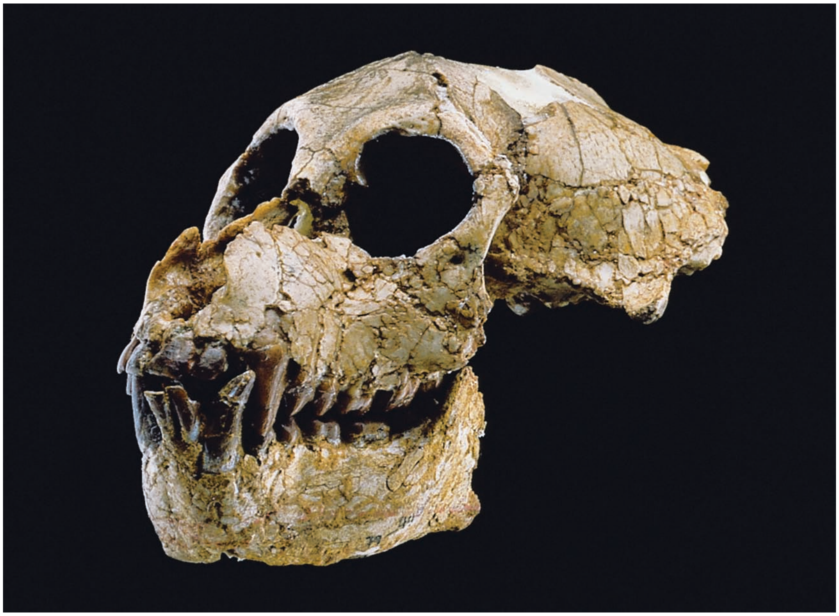


FIGURE 10.4
Skull of *Aegyptopithecus* from the Fayum in Egypt. This fossil is considered an early monkeylike form that may be ancestral to later Old World anthropoids.

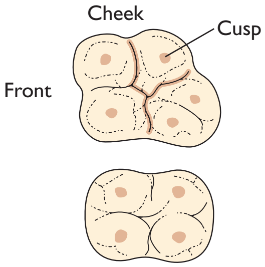


FIGURE 10.5
The Y-5 cusp pattern is found only in hominoids, and the four-cusp pattern is found in *all* anthropoids. The chewing surface is shown here. Look in the mirror, and you will probably see a Y-5 tooth, but note that not all hominid molars show this feature.

Apes appear in the fossil record about 23 mya. We refer to these earliest apes as *dental apes* because it is their teeth, rather than their overall anatomy, that resemble those of modern apes. Especially important is a feature of the molar teeth found only in hominoids and no other primates. It is called the *Y-5 cusp pattern* (Figure 10.5).

Between 23 and 5 mya, there were an estimated thirty or more different types of apes—larger-bodied, tailless, larger-brained primates. Only one lineage, however, gave rise to the modern apes and hominids. Evidence is scanty, but fossil finds point to African forms as candidates for the earliest hominoid.

Starting about 12 mya, we find fossils of more ground-dwelling, open-country apes, whose larger back teeth with thicker enamel point to a more mixed vegetable diet that included harder foods such as nuts. Fossils of these apes have been found in Africa, India, Pakistan, China, Turkey, Hungary, and Greece. One group from India and Pakistan, *Sivapithecus*, shares features with the modern orangutan and so is most likely an ancestor of that species (Figure 10.6). A new find from Ethiopia (Suwa et al. 2007) is said to be of a 10-million-year-old ancestor of modern gorillas.

Another form, *Ouranopithecus*, so far found only in Greece and dated at 10 to 9 mya, shares some features with hominids. Although clearly an ape, about the size of a female gorilla, it is thought by some to be a good candidate for a member of the ape line that eventually led to the hominids (Begun 2003).

We can't leave this discussion without noting perhaps the most famous and the biggest sivapithecid—indeed, the biggest primate ever. This giant ape, whose fossils have been found in China, northern India, and Vietnam, is called, appropriately, *Gigantopithecus* (see Figure 7.2). So far, only jaws and teeth have been found, but estimates from these indicate that this primate may have been 10 to 12 feet tall when standing upright and may have weighed from 700 to 1,200 pounds. Evidence from the teeth indicates that it was, like the gorilla, a vegetarian. *Gigantopithecus* lived from about 7 mya to perhaps as recently as 300,000 ya, recently enough to have possibly encountered modern humans. (One can't help but wonder if these creatures, or at least their bones, may have given rise to legends of the famous abominable snowman, or yeti, from the Himalayas. In any case, there is absolutely no indication that this primate still exists.)

Current evidence indicates that apes evolved in Africa and Europe about 20 mya and diverged subsequently into a number of evolutionary lines all over the Old World. Gradually these lines decreased, leaving relatively few forms to evolve into the modern hominoids. An African form

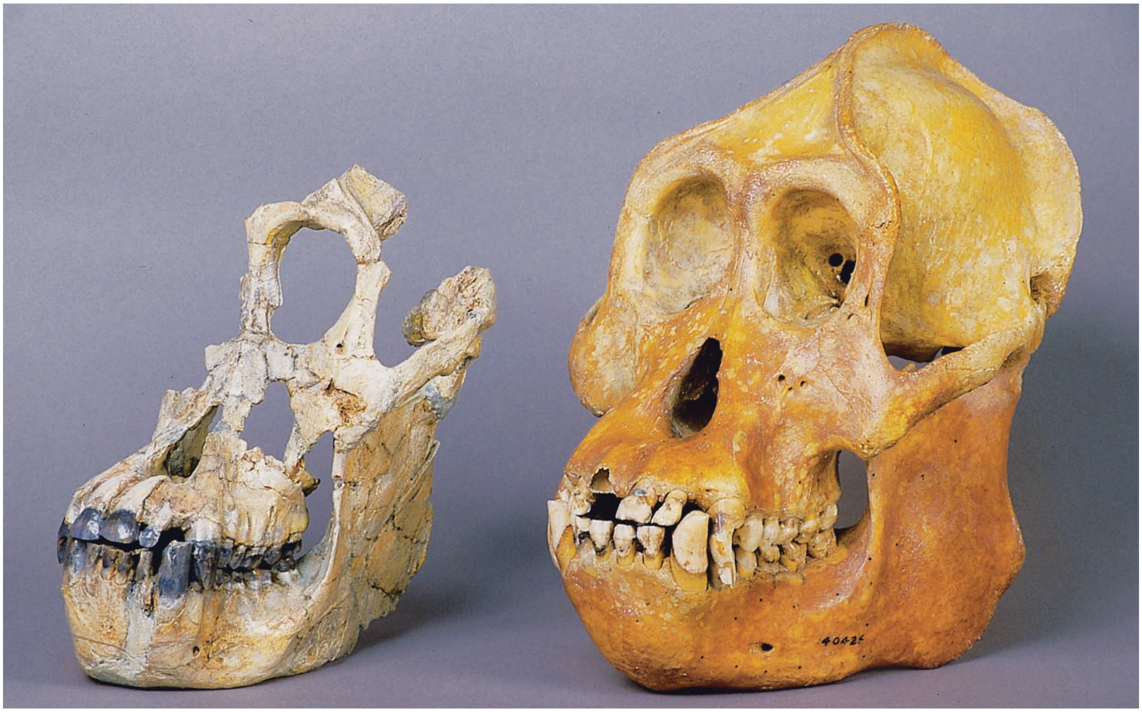


FIGURE 10.6
Skull of *Sivapithecus* (*left*) compared to that of a modern orangutan. They are essentially identical.

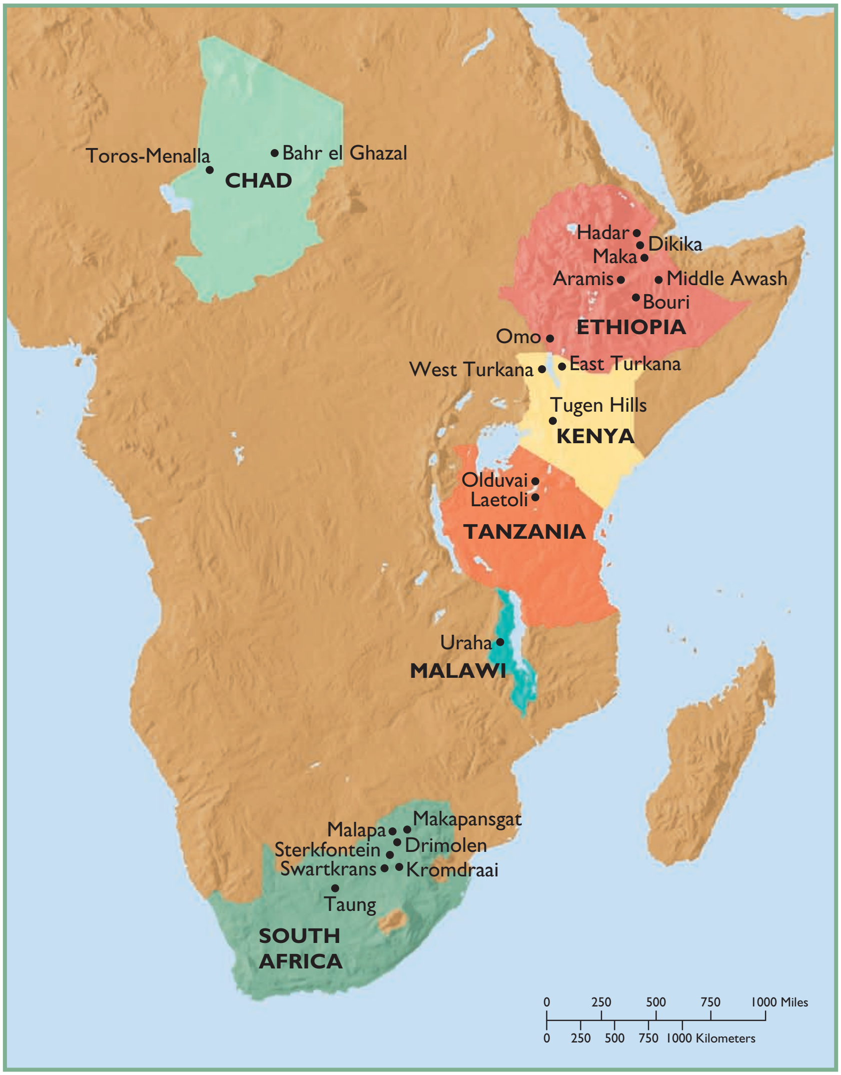
gave rise to the line leading to modern African apes and to the hominids, whose first distinguishing trait was bipedalism.

BIPEDALISM

The Benefits of Bipedalism

Not many creatures use full bipedal locomotion. Birds do—and many dinosaurs did—but they also use their tails for balance and support. Human bipedalism involves a large number of individual physical features and evolutionary changes (see Figure 9.5) and remarkable acts of coordination. When we stand and walk, with our trunk erect and knees straight, we have to balance our bodies vertically on two relatively small points of contact with the ground. We can't run particularly fast, and we aren't very stable on rough or slippery surfaces. So what could be the benefit of such a mode of locomotion, and under what environmental circumstances was it

FIGURE 10.7
Map of major early fossil hominid sites.


Toros-Menalla
Bahr el Ghazal
CHAD
Hadar
Dikika
Maka
Aramis
Middle Awash
Bouri
ETHIOPIA
Omo
West Turkana
East Turkana
Tugen Hills
KENYA
Olduvai
Laetoli
TANZANIA
Uraha
MALAWI
Makapansgat
Malapa
Drimolen
Sterkfontein
Swartkrans
Kromdraai
Taung
SOUTH AFRICA
0 250 500 750 1000 Miles
0 250 500 750 1000 Kilometers

adaptive enough to confer a reproductive advantage and so become established in our evolutionary line?

Compare the map of early hominid sites (Figure 10.7) with the map of Africa's climatic and vegetation zones (Figure 10.8). Note that the sites are now located in savannas or tropical deciduous forests (open grasslands or woodlands more open than the rain forest and with trees that undergo seasonal cycles of growth). Where these zones grade into one another, an area

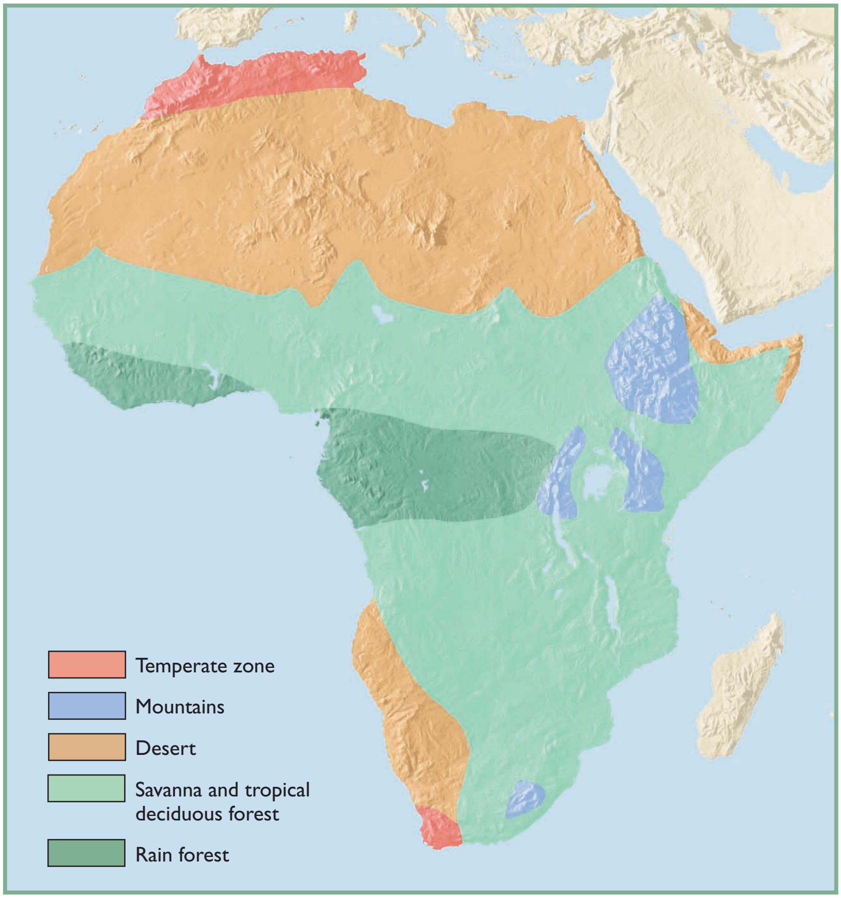


FIGURE 10.8
General climatic and vegetation zones of Africa today. Except for the large deserts in the north and south, the zones are much the same as when our evolutionary story began some 5 mya, although specific local conditions may have differed. Moreover, where zones meet, the conditions grade into one another, producing an area of mixed vegetation and other conditions.

called an **ecotone,** there is a mix of forest and open areas, as one zone grades into another. As we will see, our earliest ancestors exhibited traits associated with both bipedalism *and* an arboreal adaptation: relatively long arms; heavy shoulder girdles, arm bones, and arm muscles; and curved finger and toe bones. Perhaps in the earliest stages of our lineage, our ancestors were adapted to both a tree-climbing *and* a terrestrial, open-area way of life.

So, we may ask how bipedalism could have been a benefit in such a mix of environments, where open space intermingled with the typically arboreal environment of the primates. Several different models have been proposed.

1. ***Carrying model.*** Freeing the arms and hands from a role in locomotion would have meant that our ancestors could transport food from open areas to safer locations, such as a grove of trees or perhaps the

ecotone An area where one ecosystem overlaps and grades into another; a mixed ecosystem.

foot of a steep hill. This would have been especially important if the food were part of an animal carcass, since other meat eaters would also have found it attractive. Moreover, bipedalism would have allowed mothers to carry children in their arms while walking in search of food. Perhaps our ancestors carried sticks and rocks to throw in defense against predators or to scare scavengers away from a kill. (Chimps will occasionally hurl rocks and sticks, though not particularly accurately.) Under experimental conditions (Videan and McGrew 2000), it has been shown that having something to carry is a major stimulus for bipedal locomotion in chimpanzees and bonobos (see Figure 8.6).

2. ***Vigilance model.*** Bipedalism, by elevating the head, helped our ancestors locate potential sources of food and danger. Videan and McGrew's (2000) experiment, just noted, showed this to be an important factor in the use of bipedalism; in fact, it was the most frequent context of upright posture. It should be noted here, however, that this model only addresses upright posture, not necessarily upright locomotion.
3. ***Heat dissipation model.*** The vertical orientation of bipedalism helps cool the body by presenting a smaller target to the intense equatorial rays of the sun and by placing more of the body above the ground to catch any cooling air currents. Open spaces in Africa can be hot, and the heat built up by long periods of walking in search of food needs to be dissipated. (This factor may also explain the adaptive significance of the relatively hairless bodies of modern hominids. Having no hair allows sweat to evaporate more quickly and cool the body more efficiently.)
4. ***Energy efficiency model.*** Numerical data indicate that although bipedalism is an energy-inefficient way of running fast, compared to quadrupedalism, it is *more* efficient for walking. This, however, refers to full bipedalism. Partial bipedalism, as it was evolving, may not have conferred this advantage.
5. ***Foraging/bipedal harvesting model.*** This idea refers to the benefits of standing upright to reach sources of food on bushes and trees, particularly those difficult or impossible to climb.
6. ***Display model.*** Jablonski and Chaplin (2000) propose that the important factor of bipedalism was an upright display posture like that seen in chimps and bonobos during dominance confrontations. An upright display posture conveys meaning because it makes the individual seem larger; it is also directly related to mating success.
7. ***Walking in the trees.*** Apes use hand-assisted bipedalism when walking along branches too flexible to support their weight. They

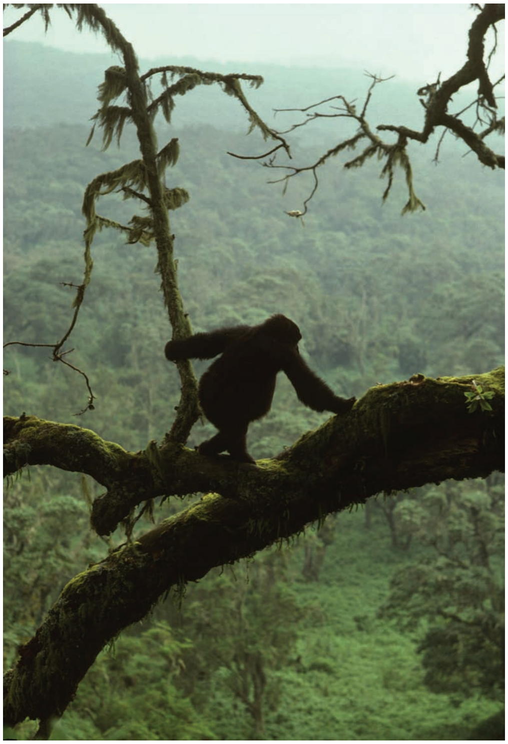


FIGURE 10.9
A gorilla uses its arms to support itself while walking bipedally along a large tree branch.

reach up and grab onto branches overhead, with their lower limbs extended (Figure 10.9). If this was true of earlier apes, it could extend bipedalism well before the hominids and redefine hominid bipedalism as "less an innovation than an exploitation of a locomotor behavior retained from the common great ape ancestor" (Thorpe et al. 2007:1328).

Each of these models has logic and evidence in its support. It seems reasonable, at the moment, to provisionally suppose that *all* these factors, acting together, could have played an adaptive role in the emergence of the hominid lineage and its characteristic mode of locomotion. But do these models explain why bipedalism would have made some individuals, and eventually some groups, more reproductively successful? *Remember that reproductive success under a given set of environmental circumstances is the measure of natural selection. Individual survival and longevity are only part of it.*

The Evolution of Bipedalism

There are two types of evidence that need to be considered here: the environments in which the relevant fossils were found and the fossils themselves.

The past 6 million years mark a period of increasing environmental fluctuation that produced great oscillations in moisture and vegetation in Africa (Potts 1996, 1998). So we can picture the boundaries of the climatic zones in Figure 10.8 as overlapping and moving as the continent got alternately wetter and drier.

Our early ancestors and some of their primate contemporaries thus encountered a variety of environments—the forest/open-space ecotone already discussed, as well as changes through time—and so underwent selection for the ability to deal with a mixed environment of increasing variability. Richard Potts calls this "variability selection"—adaptations that result in "flexible, novel responses to . . . diversity" and that "buffer" a species against "episodic change" (1998:86). The retention of arboreal features accompanied by the enhancement of bipedal locomotion seems a perfect example of this kind of adaptation. As we will see in detail, the fossils themselves, during the period we're considering, show such a combination.

In fact—again, as we will detail—there are so many fossils with demonstrated or potential bipedal abilities that bipedalism was probably "not a characteristic exclusive to the human ancestral line, but a locomotor capacity . . . found amongst some ground dwelling apes from at least 4.4 to as much as 7 million years ago" (Wells and Stock 2007).

Let's look at the specific evidence from the fossil record, and then we will return to these points at the end of the chapter.

THE EARLY HOMINIDS

The first evidence from the dawn of hominid evolution came in 1925. South African anatomist Raymond Dart was given a fossil found in a limestone quarry at a site called Taung (Figure 10.10). It took Dart seventy-three days to separate the fossil from the limestone around it. When freed, it revealed the face, braincase, and partial natural brain cast of a young primate, apelike but for three important differences.

First, the canine teeth—which are long and large in apes, with gaps to let the jaws shut—were no bigger than those of a human child.

Second was the position of the **foramen magnum.** This is the hole in the base of the skull through which the spinal cord extends from the brain and around the outside of which the top vertebra articulates. In the Taung

foramen magnum The hole in the base of the skull through which the spinal cord emerges and around the outside of which the top vertebra articulates.

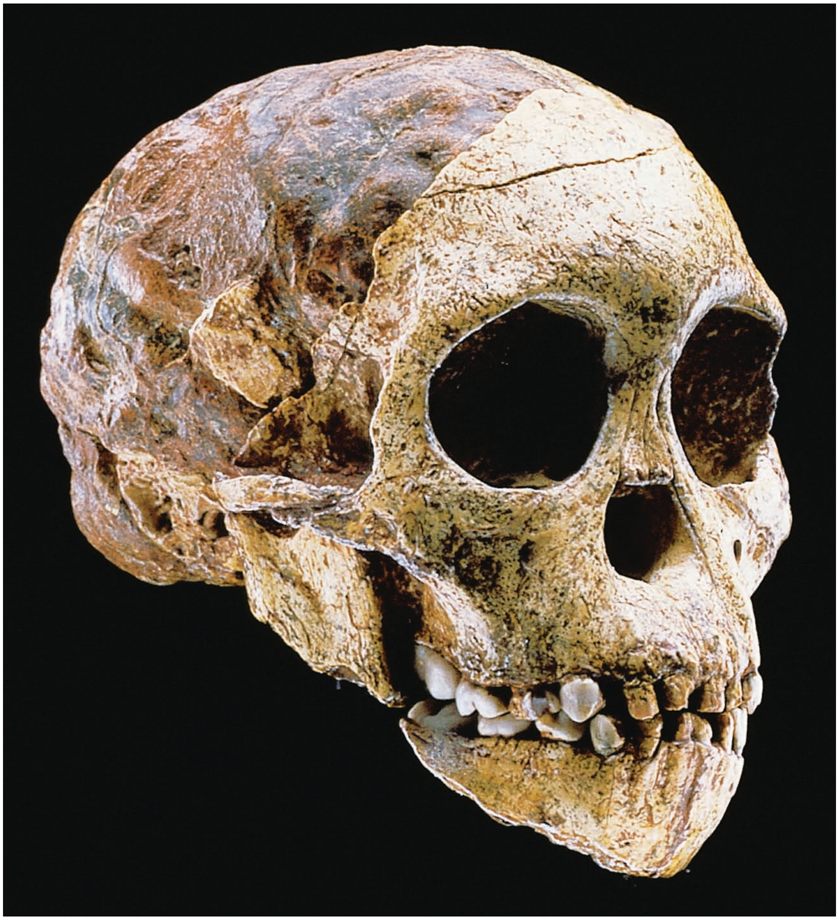


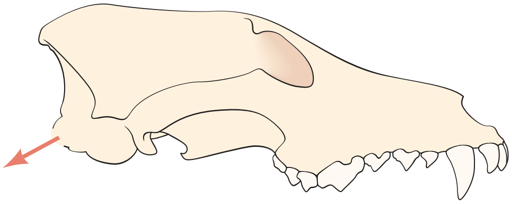
FIGURE 10.10
The "Taung Baby," the first specimen of *Australopithecus*. Note the naturally formed cast of the brain toward the back of the skull. (See also Figure 11.17.)

specimen, this hole was well underneath the skull rather than toward the back, as in apes, indicating an upright, bipedal posture rather than a quadrupedal one (Figure 10.11).

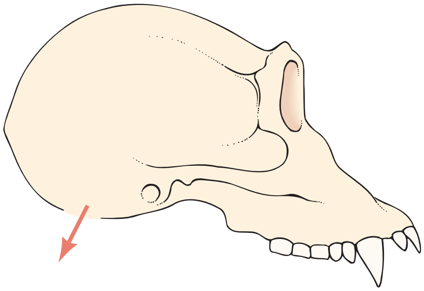
Third, Dart saw some features of the brain cast that hinted at a human direction. These have been substantiated (Falk 2009).

Dart hypothesized that the "Taung Baby," as it came to be known, was an intermediate between apes and humans. Nevertheless, he named it *Australopithecus africanus*, the "southern ape of Africa"; because of its many apelike traits, he wasn't ready to formally classify it in the human family. After all, for a quarter century or more, the expectation was that our earliest ancestors would have big brains with apelike bodies, not apelike bodies that were bipedal (see the "Contemporary Reflections" box for this chapter).

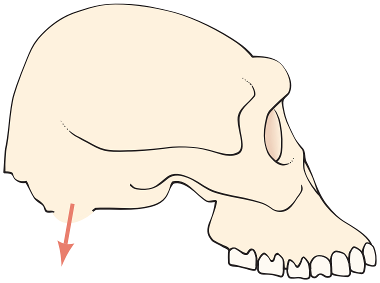
FIGURE 10.11
Comparison of the placement of the foramen magnum and orientation of the spinal column relative to the skull in a nonprimate quadruped and three primates. The wolf, with equally long fore and hind limbs, has a foramen magnum toward the back of the skull with an almost horizontal orientation of the spine. The chimp, still a quadruped but with longer arms than legs, has a more forward placement with the spine extending at an angle. In the bipedal hominids we see a trend toward a more forward placement and a vertical orientation of the spine.



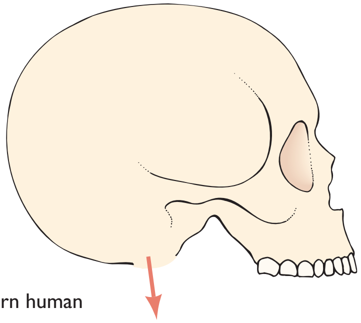
Wolf



Chimpanzee



Australopithecus



Modern human

Further finds in Africa in the following decades substantiated Dart's assessment of the anatomy of his fossil and his opinion that it represented a new type of primate. Those finds also made it clear that *Australopithecus*, rather than being an intermediary, was in fact a hominid

The story that the early hominid fossils tell is by no means clear or agreed upon by everyone. But we can begin with some reasonably well-established fossil forms and dates, which will provide a basis for understanding this period of human evolution. Then, in the following section we can examine some of the newer and more controversial fossils and consider some of the ways to put all these data together.

First, a general orientation: All the fossils discussed here belong to family Hominidae. Within family Hominidae, anthropologists can agree on three well-established groups. Only genus *Homo* still exists; the others are extinct. These groups may be defined by the following criteria, on which I'll elaborate as we continue in the chapter:

> Family Hominidae (the Hominids)
>
> Genus *Australopithecus:* small-brained; more "gracile" (graceful, slender) in the cranial features; a mixed fruit/vegetable diet; mixed bipedal-arboreal adaptive characteristics
>
> Genus *Paranthropus:* small-brained; more robust cranial features, possibly for seasonal or "fallback" use of grassland plant foods; mixed bipedal-arboreal adaptive characteristics
>
> Genus *Homo:* large-brained; generalized diet; fully bipedal; increasing reliance on culture, including tools and symbolic communication

Authorities are about evenly divided on whether *Paranthropus* is a separate genus or is part of *Australopithecus*. I will consider them separate genera. Using a different name simply helps organize our discussion of evolutionary trends during this period. More importantly, while determining species identity in the past is difficult if not impossible, and thus can be very controversial (as we will see in this and the coming chapters), a genus can be more easily defined as a "group of species . . . that share a common adaptation—variations on a single theme" (Marks 2005:51). Thus, our examination of this remote period of human ancestry will focus on the genus level.

Australopithecus

Some population of this well-known genus is almost certainly our direct ancestor. For a sense of what we know, Table 10.1 gives some detailed information for three well-established groups of australopithecines, usually

TABLE 10.1
Summary of Well-Accepted Early Fossil Hominid Species of *Australopithecus* and *Paranthropus*

	A. anamensis	***A. afarensis***	***A. africanus***	***P. robustus***	***P. boisei***
Dates	4.2–3.8 mya	3.9–3 mya	3.5–2.3 mya	2.2–1.5 mya (?)	2.2–1 mya
Sites	Lake Turkana Middle Awash	Hadar Omo Laetoli Maka Lake Turkana Dikika	Taung Sterkfontein Makapansgat Lake Turkana (?) Omo (?) Malapa (?)	Kromdraai Swartkrans Drimolen	Olduvai Lake Turkana Omo
Cranial capacity (in ml)	(no data)	380–500 mean = 440	370–515 mean = 440	520 (based on one specimen)	500–530 mean = 515
Estimated size (average, in lb)	114	110	100	105	101
Skull	Canines large, but hominid-like canine roots More apelike chin than *A. afarensis* Tooth rows parallel as in apes	Very prognathous Receding chin Large teeth Pointed canine with gap Shape of tooth row between ape and human Hint of sagittal crest	Less prognathous than *A. afarensis* Jaw more rounded Large back teeth Canines smaller than *P. robustus*, larger than *A. afarensis* No sagittal crest	Heavy jaws Small canines and front teeth Large back teeth Definite sagittal crest	Very large jaws Very large back teeth Large sagittal crest
Postcranial skeleton	Bipedal knee and ankle joints Fibula intermediate between ape and hominid	Long arms Short thumb Curved fingers and toes Bipedal	Similar to *A. afarensis* but possibly with longer arms and shorter legs	Hands and feet more like modern humans Retention of long arms	Similar to *P. robustus*

considered to be different species. There are at least three other suggested species of genus *Australopithecus* (look ahead to Figure 10.23). As noted above, determining species among fossils is difficult if not impossible. The ultimate test—fertility—obviously cannot be conducted, so we are left with deciding if phenotypic differences warrant a species distinction. Such decisions depend on what differences one looks at and how important one thinks they are. In the end, the debate over species in the fossil record often just confuses the issue, so, as noted, we will focus here on the genus level and summarize our knowledge and conclusions.

Perhaps the most famous, and certainly most complete, member of this genus is "Lucy" (named after the Beatles's song), the type-specimen of *Australopithecus afarensis* (that is, the specimen that established the species). She was found in 1974 by Donald Johanson and his team in Ethiopia (Figure 10.12). Lucy is remarkable because, at 3.2 million years old, nearly 40 percent of her skeleton was preserved, and all parts of her body, except her cranium, were well represented. Lucy herself is small, standing only 3 feet 8 inches and weighing about 65 pounds. But no australopithecine was much heavier than 100 pounds or stood much more than 5 feet. Here are the general characteristics of the genus:

Geography and Time As you can see from Table 10.1 and the map in Figure 10.7, fossils classified in this genus are found in East Africa, southern Africa, and north central Africa (Chad). The time range is 4.2 mya to 1.9 mya, a little over 2 million years.

Cranium Lucy's cranium was incomplete, but there are sufficient cranial fossils from this genus to know what they looked like (Figure 10.13). Average brain size for the genus is about 440 ml (a 12-ounce can of soda

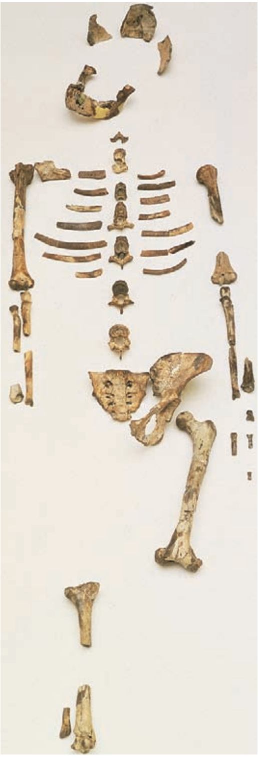


FIGURE 10.12
Skeleton of "Lucy," the first specimen of *A. afarensis.*

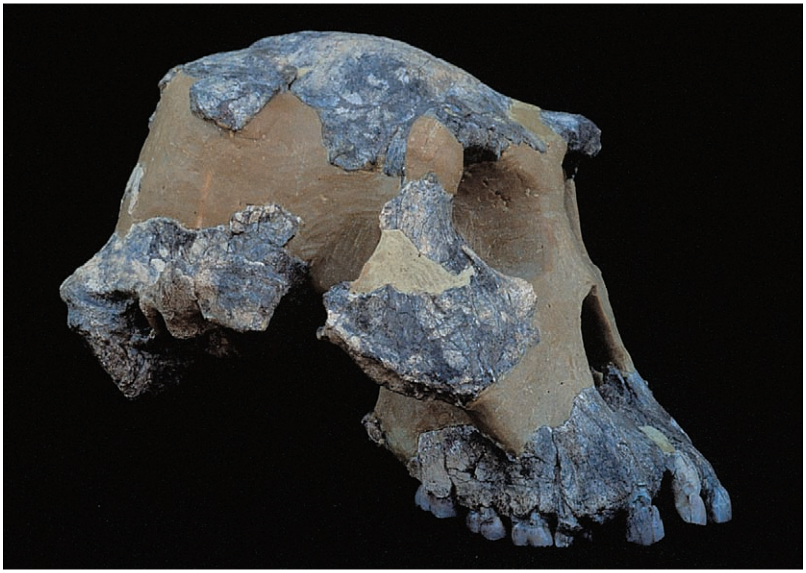
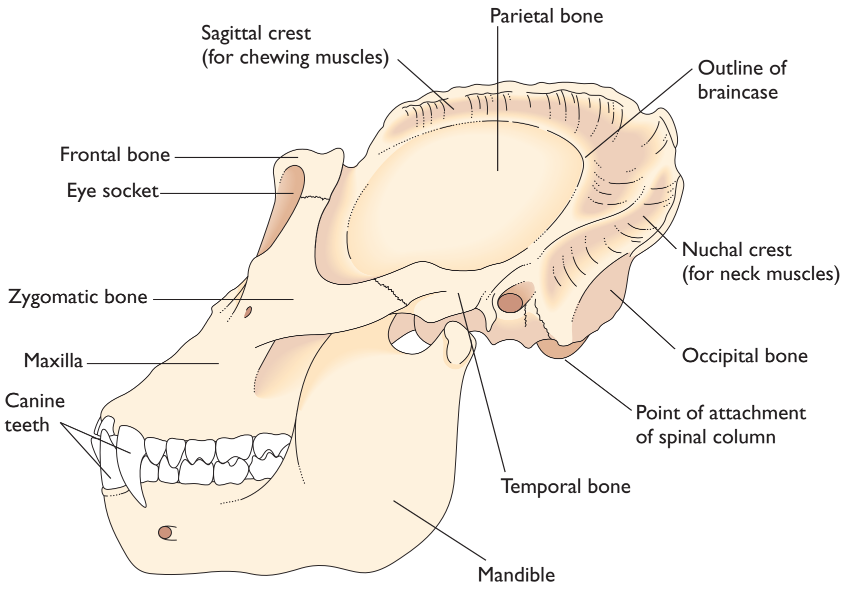


FIGURE 10.13
Side view of cranium of *Australopithecus afarensis*. Spaces created by missing bones have been filled in using information from other specimens and knowledge of related species.

FIGURE 10.14
Skull of a male gorilla. Compare the sagittal crest with those in Figures 10.17 and 10.18.


Sagittal crest
(for chewing muscles)
Parietal bone
Outline of
braincase
Frontal bone
Eye socket
Zygomatic bone
Maxilla
Canine
teeth
Nuchal crest
(for neck muscles)
Occipital bone
Point of attachment
of spinal column
Temporal bone
Mandible

holds 355 ml) with a maximum of about 500 ml. This is approximately the brain size range of chimpanzees. (The modern human range is 1000 to 2000 ml.) In some specimens of *Australopithecus*, there is an indication of a ridge of bone along the top of the skull for the attachment of major chewing muscles, the **sagittal crest.** Gorillas have a pronounced crest (Figure 10.14).

Face and Dentition The face of *Australopithecus* displays **prognathism,** a jutting forward of the lower face and jaws. This condition is also found in the African apes and is associated with powerful chewing forces. Compare Figures 10.13 and 10.14. As in apes, the canine teeth are long and pointed and there are gaps in the tooth rows to accommodate these long teeth when the mouth is closed. These features, however, are not as extreme as in the apes. The tooth row itself is intermediate between the parallel back teeth of apes and the divergent rows of modern humans (Figure 10.15).

sagittal crest A ridge of bone, running from front to back along the top of the skull, for the attachment of chewing muscles.

prognathism The jutting forward of the lower face and jaw area.

Postcranial Skeleton The bones of the pelvis, legs, and feet indicate habitual bipedalism. At the same time, the relatively long arms, heavy musculature of the arms and shoulders, and curved finger bones point to the retention of arboreal abilities, a mixed adaptation to a mixed environment, as pointed out before. The bipedal abilities of the australopithecines

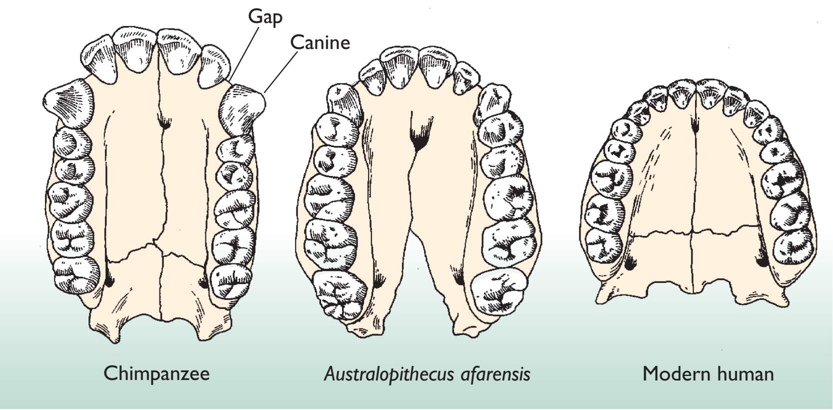


FIGURE 10.15
Comparison of upper jaws and tooth rows of chimpanzee, *Australopithecus afarensis,* and modern human. Note the parallel postcanine teeth in the chimp, the slightly divergent tooth row in the early hominid, and the divergent row in the modern human. Note also the large canines and the large gap (*diastema*) in the chimp, the lack of these in the modern human, and the intermediate state in the early hominid. *Australopithecus anamensis* had slightly larger canines than the later *A. afarensis* and tooth rows more like the ape.

are confirmed by a unique set of footprints from Tanzania, dated at 3.7 mya. They were left in new volcanic ash that quickly hardened. They clearly show the marks of two individuals who had a very humanlike stride (Figure 10.16, along with a reconstruction of the pair). We also see phenotypic characteristics that indicate sexual dimorphism even back then. Lucy was assessed to be a female because of the kinds of traits discussed in Chapter 9.

Behavior The anatomy of the fossils and the mixed ecology of the areas in which they lived have established that they were most likely both arboreal and terrestrially bipedal, giving them an adaptive flexibility to mixed and changeable conditions. Related to this are indications of the type of diet they may have found in such conditions. Microscopic analysis of tooth wear patterns points to a mixed vegetable diet of fruits and leaves. Carbon isotope (^{13}C) analysis of tooth enamel hints at small animals that might have been hunted, or larger ones that were scavenged (Sponheimer and Lee-Thorp 1999). There is also evidence that they might have dug up rootstocks (Ragir 2000) and opened termite mounds (Holden 2001a). In other words, australopithecines ate a diet much like that of modern chimps and bonobos (minus the carcass eating, which those species don't do).

A new, and still controversial, possibility is that some australopithecines may have used simple stone tools to help in scavenging. From a 2.5 million-year-old site in Ethiopia (Bouri on the map in Figure 10.7), come some fossils that are put into a new species (*A. garhi)* and some bones of prey animals with possible stone tool cut marks. These, however, might have been made by another hominid, as we will discuss in the next chapter.

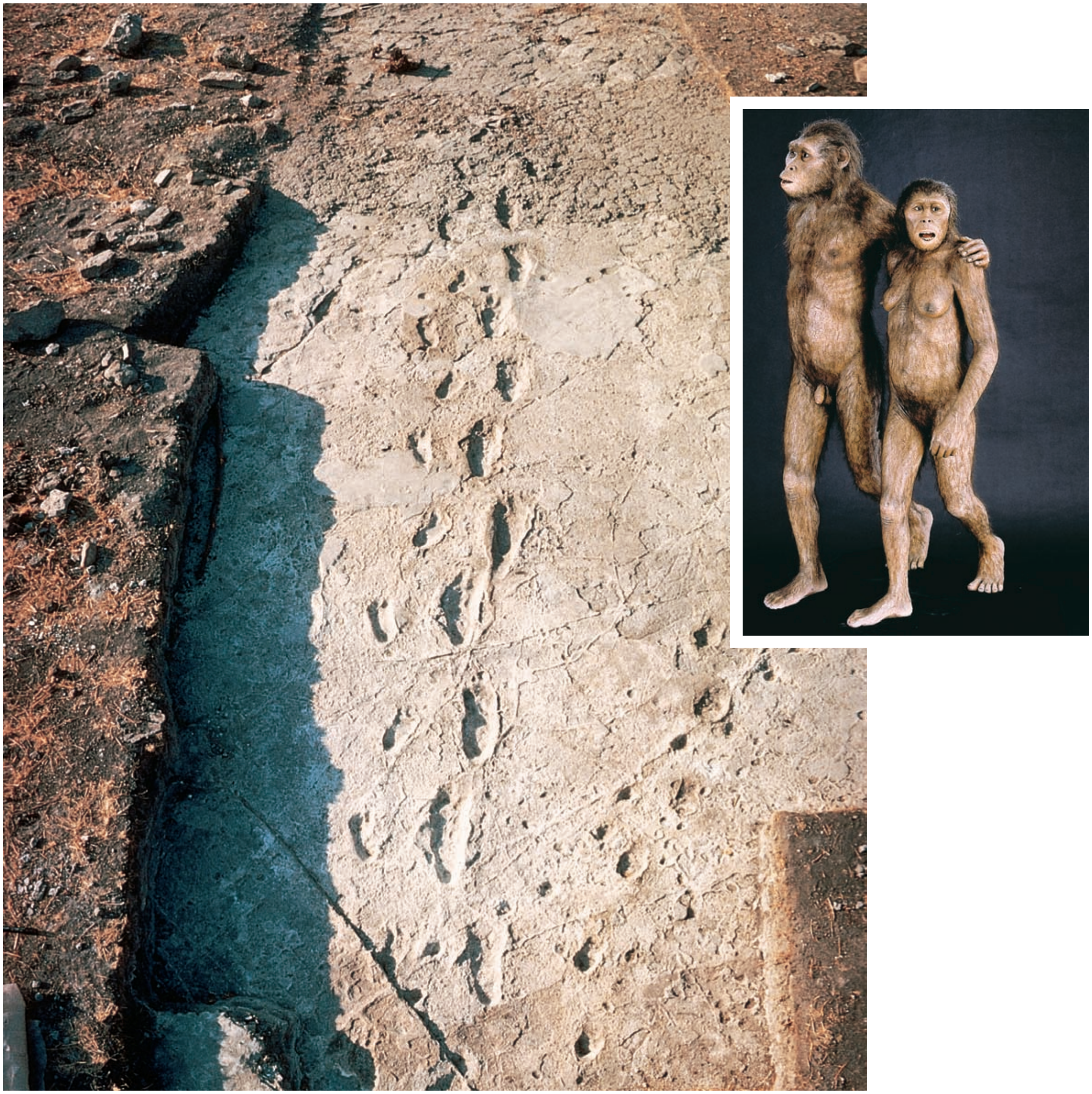


FIGURE 10.16
The larger photograph shows the Laetoli footprints from Tanzania. The inset shows a reconstruction from the American Museum of Natural History in New York City of male and female *A. afarensis,* who are thought to have made these footprints.

Over their 2.4 million year tenure, *Australopithecus* showed some evolutionary changes. Faces became a little less prognathous, the sagittal crest disappeared, canine teeth became smaller and the gap in the tooth row closed, and the tooth row became more rounded (see Figure 10.15). The genus disappears from the fossil record at about 1.9 mya.

Paranthropus

There are three proposed species of this genus. Two are detailed in Table 10.1; the third is represented by a single cranium (Figure 10.17) and some fragmentary remains. About the same overall size as *Australopithecus*, they had slightly larger brain sizes and, most notably, a robusticity of the areas of the cranium involved with chewing. *Paranthropus* is generally considered a branch off of the australopithecines, as is our genus, *Homo*. We are, then, evolutionary cousins.

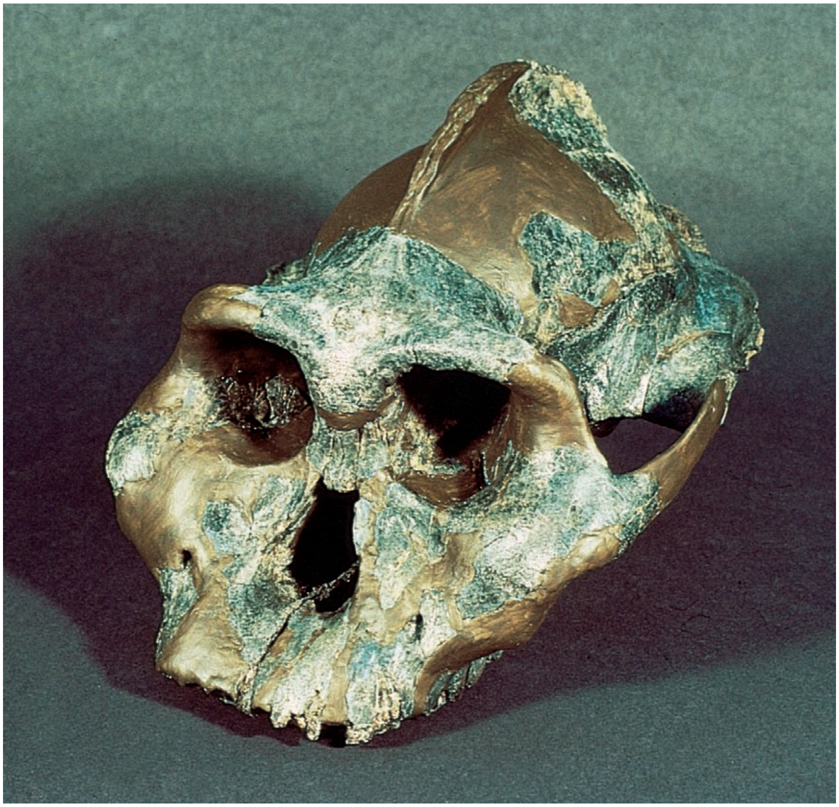


FIGURE 10.17
The "Black Skull," *Australopithecus aethiopicus,* is a possible ancestor of *P. robustus* and *P. boisei.* It shows a great degree of prognathism and the largest hominid sagittal crest.

Geography and Time Fossils of this genus have been found in eastern and southern Africa (see Table 10.1 and Figure 10.7). They range in age from 2.8 to 1.0 mya.

Cranium Brain size ranges from 410 ml to 520 ml, a slightly larger average than the australopithecines. A large sagittal crest, an attachment for chewing muscles, runs along the top of the skull.

Face and Dentition All the features associated with chewing are large: large cheekbones (another attachment area for chewing muscles), broad dished-out face, huge mandible, and large teeth overall with back teeth larger relative to the front teeth (Figure 10.18).

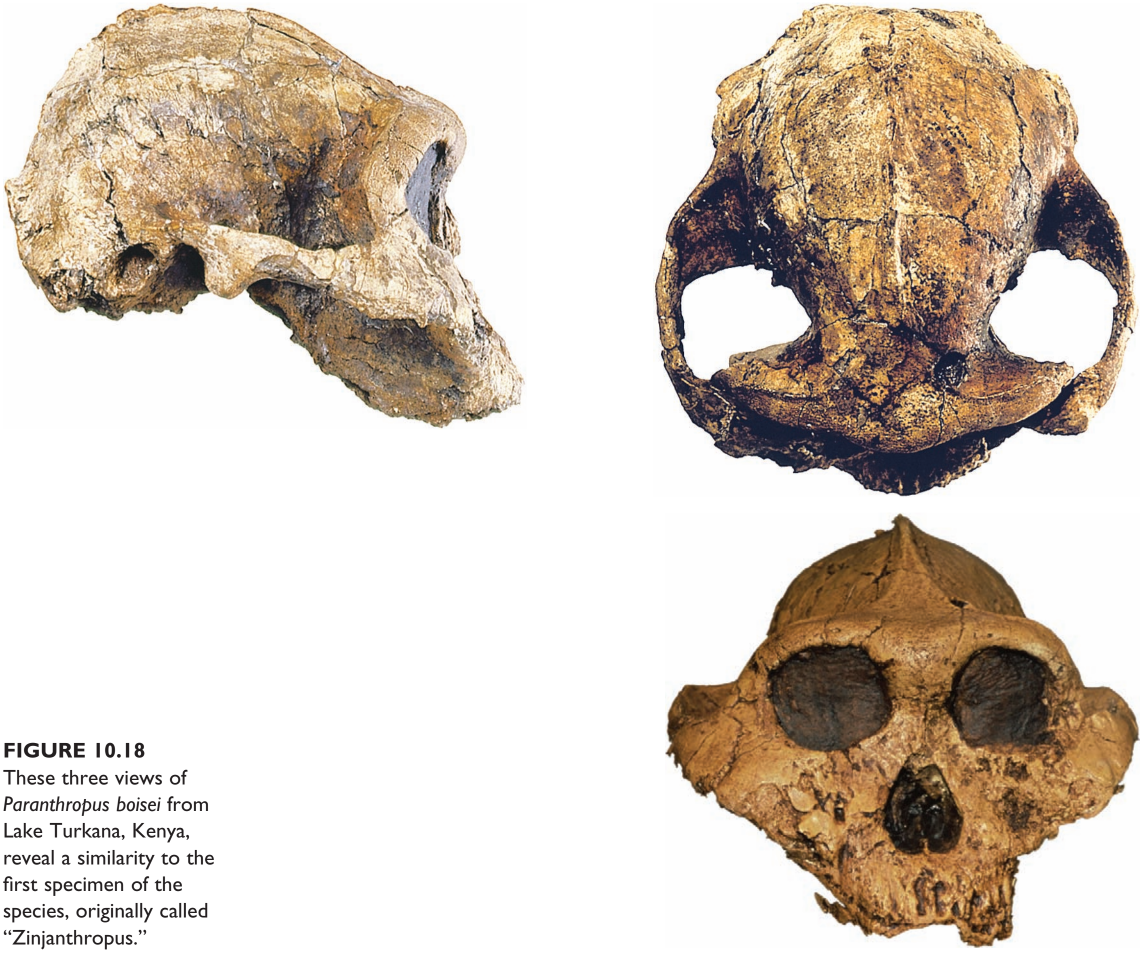


FIGURE 10.18
These three views of *Paranthropus boisei* from Lake Turkana, Kenya, reveal a similarity to the first specimen of the species, originally called "Zinjanthropus."

Postcranial Skeleton Much the same as *Australopithecus*, the relatively long arms and heavy upper arms and shoulders are signs of the retention of arboreal adaptations. The pelvis and legs, however, clearly indicate habitual bipedalism.

Behavior *Paranthropus* fossils are more associated with open savanna areas than are those of the australopithecines. Wear-pattern analysis of the teeth indicates a variable diet with lots of hard items such as seeds, nuts, and tubers being at least a "fallback" diet seasonally or during hard times. It appears, in fact, as if dietary variability increased in this genus during its almost 3 million year tenure.

As we will discuss soon, it appears as if *Paranthropus* was a response to an environmental change around 3 mya—to drier conditions—a change that may also have stimulated the evolution of our own genus. *Paranthropus* is gone from the fossil record by a million years ago.

THE SEARCH FOR THE FIRST HOMINIDS

There are four early fossil forms that have been touted by their discoverers and others to be major steps in the evolution of the hominids in general or of genus *Homo* in particular. These claims, not surprisingly, are not without disagreement.

Ardipithecus

In 1992 and 1993 in Ethiopia, seventeen fossil fragments were discovered, including some arm bones, two skull bases, a child's mandible, and some teeth. The fossils were said to be different enough from any found previously to warrant creating a fourth hominid genus and a new species, *Ardipithecus ramidus* (the genus name means "ground ape" and the species name "root" in the Afar language). The fossils were dated at 4.4 mya. In 1994 more fossil bones were recovered in Ethiopia, close to the first site. These consisted of ninety fragments representing about 45 percent of a skeleton (Figure 10.19).

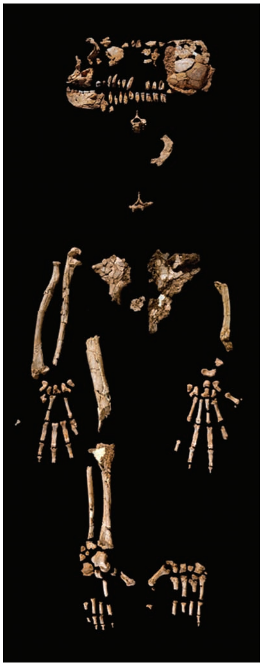


FIGURE 10.19
The skeleton of *Ardipithecus ramidus*. It is of a female who stood about 47" tall and lived 4.4 mya. Assessment of this species (see text) is largely based on these remains.

It took until 2009 for the full report on *Ardipithecus* to be published (White et al. 2009, and other articles in the 2 October issue of *Science*), and the conclusions are interesting and important to our story. Morphologically, "Ardi," as she is called, had a brain size of 300 to 350 ml, a little under the average for a chimpanzee. While we might expect Ardi to be apelike with the beginnings of human features, the facts are surprising. She was prognathous but not as much as apes. Her cranium sat atop her spine, as in hominids and unlike apes. Her canines were smaller than in modern apes, and her hands and wrists show that she put her weight on her palms, not on her knuckles as modern apes do. Her big toe was divergent from the others but her feet were flat, unlike in modern apes. Her lower pelvis was apelike, with features that would have aided climbing, but her upper pelvis was structured for bipedal walking when on the ground.

In short, she was a unique combination of traits, not some intermediate between modern apes and humans. Put another way, she shows we cannot assume the last common ancestor of humans and chimps was chimplike. Rather, both humans and chimps are specialized forms that evolved along different pathways from a common ancestor, who was probably much like Ardi.

Further, Ardi supports the idea that bipedalism evolved first in the forests, giving our remote ancestors a mixed adaptation—the best of both worlds—to both arboreal and terrestrial living. The remains of *Ardipithecus* were found in areas that were woodland when they were alive.

Finally, it should be noted that not everyone readily agrees with this interpretation. Some question just how bipedal Ardi was. Others question the conclusion that remote human ancestors were never chimplike. Debate continues, but that's how science progresses.

There is a second proposed species of *Ardipithecus*, *Ardipithecus kadabba* (*kadabba* means "base family ancestor" in the Afar language). Found in 2004 in the same Ethiopian location as *Ard. ramidus,* these fossils are older, 5.8 to 5.2 mya, and comprise a mandible, teeth, partial clavicle, hand bones, and, most important, a toe bone that seems to indicate bipedalism. A common interpretation is that *Ardipithecus kadabba* is ancestral to *Ard. ramidus.* The interpretation, of course, is not without controversy; some authorities even claim these fossils represent chimpanzee ancestors.

Kenyanthropus

In March 2001 Meave Leakey, daughter of Louis and Mary Leakey, announced a new hominid genus (Leakey et al. 2001). It is based on a fairly complete, although badly distorted cranium and mandible, found in 1998 and 1999 in Kenya and reliably dated at 3.5 mya (Figure 10.20). The fossils are said to show a new combination of features. The brain size, some dental features, and details of the nasal region are like those

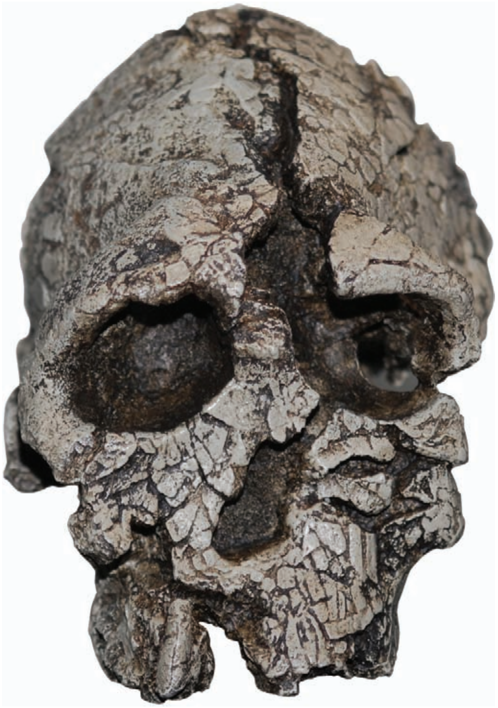


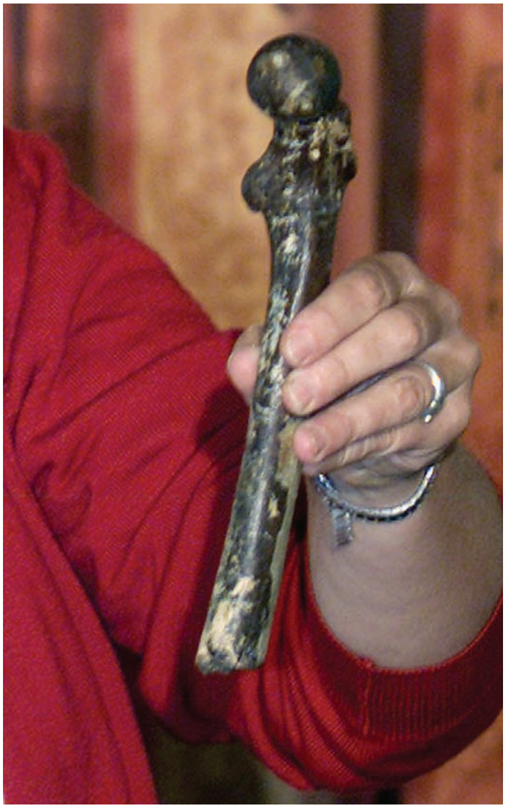
FIGURE 10.20
The skull of *Kenyanthropus platyops*.

of genus *Australopithecus*, but its face appears flat, it has a tall, vertically oriented cheek area, and shows no depression behind the brow ridges. In these ways, it bears a resemblance to an early form of genus *Homo* (see Figure 11.4). This set of traits led its discoverers to give it a new genus and species name—*Kenyanthropus platyops* ("flat-faced hominid from Kenya"). Some authorities have suggested that this new form may be a better common ancestor for *Homo* than any species of *Australopithecus*. Others say it is a member of genus *Australopithecus* (White 2003).

Orrorin

In October 2000 an even older possible hominid ancestor was proposed by French paleoanthropologists (Balter 2001b), based on thirteen fossil fragments from the Tugen Hills in northwestern Kenya. The dating of these fossils—femurs, teeth, portions of a mandible—is 5.6 to 6.2 million years (Figure 10.21). Their identity, however, is a matter of debate. The discoverers claim that the fossils represent the real ancestor of modern humans and that *Australopithecus* is a branch. *Ardipithecus kadabba*, they say, is a chimp ancestor. They base their claim on their assessment that this hominid *Orrorin tugenensis* (*orrorin* means "original man" in the local dialect)

FIGURE 10.21
The femur of *Orrorin tugenensis,* which appears to indicate bipedalism.



was bipedal and exhibited expressions of certain traits that were more modern than those of other early hominids. Its bipedalism has recently been supported by further study of the femurs (Richmond and Jungers 2008). Other authorities disagree with this analysis, and some question whether this form even *is* a hominid (Haile-Selassie 2001).

Sahelanthropus

The most recent candidate for "first hominid" is a find from the Toros-Menalla site in northern Chad consisting of a cranium, jaw fragment, and several teeth and dated from 7 to 6 mya (Figure 10.22; Brunet et al. 2002, 2005; Zollikofer et al. 2005). It has been placed in a new genus and species, *Sahelanthropus tchadensis* (after the Sahel region of Africa that borders the southern Sahara) and is known popularly as "Toumaï" ("hope of life"

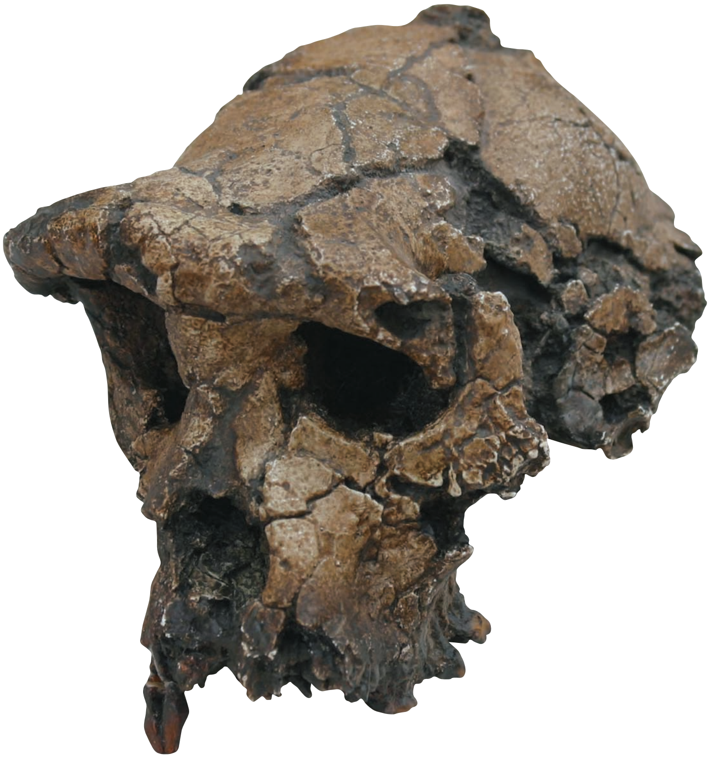


FIGURE 10.22
The cranium of *Sahelanthropus tchadensis*.

in the local Goran language). This form is described as having a "mosaic" of features. It is very apelike in its brain size (estimated at 320 to 380 ml), widely spaced eye orbits, and other details of its morphology, but with a number of striking features characteristic of later hominids. These include small canines of a hominid size, shape, and wear pattern; a face with reduced prognathism; and a continuous brow ridge. The forward position of the foramen magnum, while not enough evidence to reliably infer habitual bipedalism, still makes such an inference "not . . . unreasonable" (Brunet et al. 2002:150). The primary investigators thus claim that this form represents "the oldest and most primitive known member of the hominid clade, close to the divergence of hominids and chimpanzees" (151).

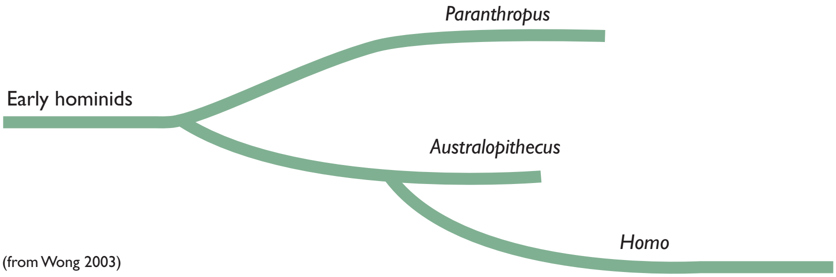
This view, of course, has its detractors. One group (Wolpoff et al. 2002) claims that this form was not bipedal and, indeed, "was an ape" (582). (See Brunet 2002 for a counterargument.)

As is evident, research into the earliest phases of hominid evolution continues. As the epigraph of this chapter indicates, our origin will probably always be enigmatic. But we are slowly filling in the gaps.

PUTTING IT ALL TOGETHER

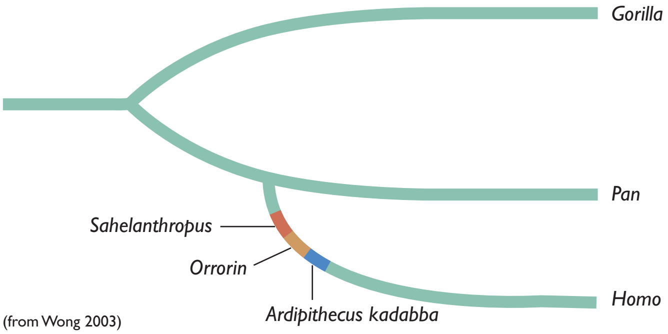
Connecting the Dots

Figure 10.23 shows the dates of all the established and proposed early hominid fossil species, the most important of which are discussed in this chapter (with *Homo* added for perspective and a preview of what's to come). A number of different specific models have been proposed for connecting all these fossils into an evolutionary tree. Most authorities generally agree that the hominids from about 4 mya on can be grouped into two natural categories, *Australopithecus* and *Paranthropus*. There is also general agreement that it was some member of *Australopithecus* that gave rise to *Homo*. A simple tree, then, would look like this:



(from Wong 2003)

There is a difference of opinion as to *which* australopithecine, if there are several species, is the direct ancestor of *Homo*, and authorities have different favorite candidates. But there is even more debate over the newest fossil finds: *Ardipithecus kadabba*, *Orrorin tugenensis*, and *Sahelanthropus tchadensis*. With relatively scanty evidence so far, and with different body parts represented by the existing fossils, comparison and analysis are necessarily very tentative. At one extreme (see Wong 2003) is the idea that those three are lineal descendants, all on the line to *Homo*:



(from Wong 2003)

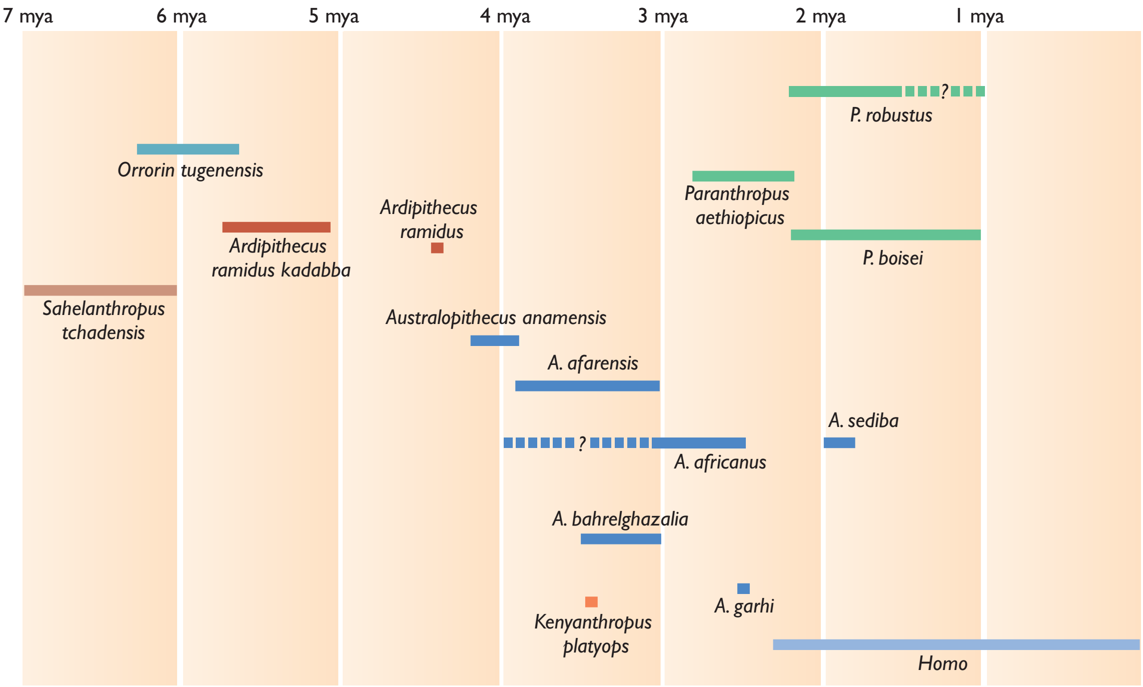
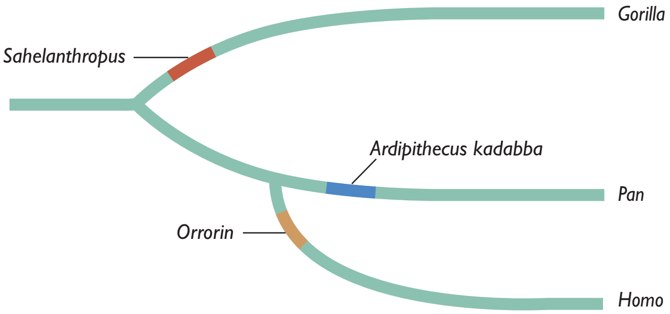


FIGURE 10.23
The fossils discussed in this chapter with their currently accepted time ranges. The dashed lines indicate possible extensions of those ranges.

The opposite extreme has the three representing ancestors of three different genera:

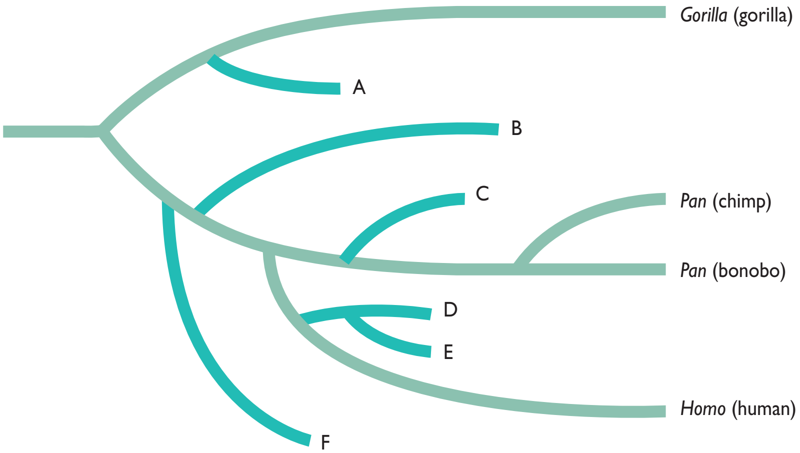


(from Wong 2003)

Note, however, that all existing models assume that the basic tree is formed by connecting the three *living* genera—*Gorilla*, *Pan*, and *Homo* and then placing all fossil species on the resulting lines, or maybe connecting them as branches from those lines. But perhaps the fossils in Figure 10.23 are related in a more complex fashion.

Perhaps some of these fossils, even if they were bipedal, were, literally, bipedal apes; the phrase could be more than a physical description of

FIGURE 10.24
Hypothetical tree of hominid evolution. *A* through *F* represent extinct forms. Perhaps, say, *B, D, E,* and *F* show evidence of bipedalism, but note that *B* and *F* are not connected to the hominid line. Thus, bipedalism does not necessarily place a fossil in our family.



some of our early ancestors. It might be taxonomically accurate. In other words, bipedalism might have evolved more than once and in evolutionary lines that are not directly connected to the hominids. Put another way, bipedalism—while a distinction of humans *at present*—might not be an exclusive characteristic of the beginning of our line (Figure 10.24). What are my reasons for proposing this? There are two.

Bipedalism Is Not Unknown in the Apes All the African great apes are capable of bipedal standing and walking, and a recent study (Stanford 2006) has shown that postural (as opposed to locomotor) bipedalism is common in chimpanzees as they stand to forage in and from trees. The same is true for orangutans. The precursor of locomotor bipedalism, in other words, is exhibited by apes and could have evolved to a more refined state in some ape lines, for all the adaptive reasons we have hypothesized for that evolution in humans (Wood and Harrison 2011).

Bipedalism Differs between Genera *Homo* and *Australopithecus* *Homo*, it seems, is built not only for bipedal walking but for bipedal endurance running as well, a trait that would also be potentially useful on the African plains and elsewhere (Bramble and Lieberman 2004; Summers 2005).

The attachment point of our Achilles tendon and the full arch of our feet, both different in chimps and *Australopithecus*, aid in a bouncing gait, a more energy-efficient way to run long distances. Our large gluteus maximus (butt) muscles help stabilize our hips while running; chimps and *Australopithecus* show more stable shoulders than hips. And *Homo* has muscle attachments, lacking in chimps and the australopithecines, that keep our heads steady while running, as well as modifications of the semicircular canals in the ears that keep us balanced by telling us, essentially, which way is up.

Put in evolutionary terms, then, these adaptations for endurance running are derived characteristics of *Homo* and are seen in early *Homo erectus* (the first undisputed member of our genus) and perhaps in even earlier *Homo habilis* (see Chapter 11; Bramble and Lieberman 2004:351). Thus, *Homo* is characterized not only by habitual bipedalism but also by a *kind* of bipedalism *different from* that of earlier hominids. So our current mantra—"If it's a biped, it must be human or a human ancestor"—might not be true, and perhaps the only sure sign of a fossil on our evolutionary line might be the body plan associated with *Homo* (including our *type* of bipedalism) and the beginnings of an enlargement of the brain. Connecting all the fossils shown in Figure 10.23 is, then, currently premature, because we simply don't have enough evidence.

The Ecological Context

What might have caused the branching that founded the new genera of *Paranthropus* and *Homo*? What caused the extinction, around the same time, of genus *Australopithecus*? Finally, what might have caused the extinction of *Paranthropus* about 1 mya?

We can't answer these questions with certainty, but recall Richard Potts's evidence for a sharp increase in environmental variability in Africa starting about 6 mya and continuing—and further increasing—through time (1996, 1998). There is also evidence for a major and abrupt change about 2.8 mya—an intensification of cycles that produced a shift toward grasslands (Kerr 2001; de Menocal 2011). Increased environmental variability resulting in a series of newly emerging, complex, and diverse habitats may have initially promoted different adaptations among hominid populations, as seen in the branching that gave rise to the robust hominids and to *Homo*. But if the degree of the fluctuations continued to increase, this may have put such pressure on the hominid adaptive responses that those groups less able to cope eventually became extinct. Unable to survive well enough to perpetuate themselves in the face of decreasing resources, these now-extinct hominids were possibly outcompeted for space and resources by the better adapted, a phenomenon known as **competitive exclusion.** In this case, only the adaptive response that included the ability for endurance running and an increase in brain size, with its concomitant increase in ability to understand and manipulate the environment, proved successful in the long run. We turn to the story of these adaptive responses next.

competitive exclusion What occurs when one species outcompetes others for the resources of a particular area.

Contemporary Reflections

Is There a "Missing Link"?

A headline in the 19 December 1912 issue of the *New York Times* proclaimed, "Paleolithic Skull Is a Missing Link." The skull referred to was the now-infamous "Piltdown Man," discovered in England, named *Eoanthropus* (the "dawn man")—and forty years later shown to be a fraud (see Feder 2010 for details). At the time, however, it was touted as the "missing link" because it possessed traits that were a perfect mix between those of human and ape. Its cranium was the shape and size of a modern human's, and its mandible was decidedly apelike. In fact, the cranium *was* of a modern human and the jaw *was* of a modern orangutan—modified by the still-unidentified perpetrator to appear ancient.

For much of the history of evolutionary thought, evolution was conceived of as a ladder or a chain, progressing from primitive to modern, with living forms representing points on that chain. Even when it was generally acknowledged that humans had descended from apes, this evolution was thought of as unilinear—a single line of progress from ape to man. Thus, as we go back into the fossil record, we should eventually find something that is intermediate—half ape and half human. Since modern apes were thought of as the remnants of primitive forms that had never evolved further, the missing link (notice the chain metaphor) was conceived of as a mix of the traits of *modern* humans and *modern* apes. In our hubris, we were sure it was our big brains that separated us from the apes and that had evolved first, so the combination fabricated to concoct the Piltdown skull fit the bill perfectly. It had that big-brain hallmark of humanity, perched on top of an otherwise apelike jaw.

Indeed, even when evolution was recognized as being a branching tree rather than a ladder or chain, the idea of fossil forms that were intermediates between modern species still held. Famed anatomist Sir Arthur Keith wrote that "to unravel man's pedigree, we have to thread our way, not along the links of a chain, but through the meshes of a complicated network" (1927:8). Then, on the next page, he accepted the Piltdown find as authentic.

We recognize today that living species are not leftover primitive links on an evolutionary chain but are, themselves, the products of evolution. A missing link in the traditional sense—between modern humans and modern apes—simply does not exist. What *does* exist is a common ancestor of humans and our closest relatives, the chimpanzees and bonobos—and it did not look exactly like any of those modern species. Granted, we have reason to think that the common ancestor resembled a bonobo or chimp more than a modern human, but this is just because evolution happened to take place at a more rapid pace in hominids than in the apes. The apes are still modern species.

So what we *can* look for is that common ancestor. It is a "link" not in the sense of a chain, but in the sense of being that point where our two evolutionary lines converge. At the moment, that form is still missing.

What will it look like? It should have characteristics shared by both modern hominids and apes, but it will look, on the whole, like neither. It could be one of the forms we know about (see Figure 10.23), or it could be a form yet to be discovered.

SUMMARY

The primates are one of the earliest of the existing mammal groups to evolve. They appear to have evolved first in what are now North America and Europe, but the success of their adaptations allowed them to radiate over the Old World and into the New World.

About 23 mya, the hominoids appear in the form of primitive apes. This successful group has left fossils all over Africa, Europe, and Asia. It is from one of the African apes that our family, Hominidae, branched off probably 6 to 5 mya.

The evolution of habitual bipedalism is thought to mark the beginnings of our family and was the major distinguishing characteristic of this family for the first half of its time on earth. Bipedalism may have begun as part of one group's adaptation to the forests. However, these adaptations would also prove useful in Africa's increasingly variable environment, and the hominids soon were well established and radiated into three distinct groups, best classified as separate genera: *Australopithecus*, *Paranthropus*, and *Homo*.

The first two genera, *Australopithecus* and *Paranthropus*, with their chimp-sized brains, remained largely vegetarian and persisted until nearly 1 mya. They eventually lost out to a combination of environmental change and competition from the third hominid genus, *Homo*, with its bigger brain and ability to manipulate its environment. Our genus is the subject of the next chapter.

QUESTIONS FOR FURTHER THOUGHT

1. People often ask this logical question: If humans are descended from apes, then how come there are still apes? How would you respond to this?
2. Looking at the fossil record of the hominids, we see that the hominid line that survived after about 1 mya was the one with the big brain. From our perspective, this makes it seem as if our evolution was inevitable. Is this the case? Would the big-brained species have been successful in all circumstances? Once the evolution of hominids got started, were *we* a predictable result?

KEY TERMS

ecotone

foramen magnum

prognathism

sagittal crest

competitive exclusion

SUGGESTED READINGS

The primates and their evolution are covered in John G. Fleagle's *Primate Adaptation and Evolution*. The intriguing story of *Gigantopithecus* is told in *Other Origins: The Search for the Giant Ape in Human Prehistory*, by Russell Ciochon, John Olsen, and Jamie James.

The story of the study of the human fossil record and of some of the major discoveries is told in *Lucy: The Beginnings of Humankind*, by Donald Johanson and Maitland Edey, and in a sequel, *Lucy's Child: The Discovery of a Human Ancestor*, by Donald Johanson and James Shreeve. Both of these books are somewhat outdated but still convey the excitement of paleoanthropology. A slightly different perspective on much of the same material is found in Richard Leakey and Roger Lewin's *Origins Reconsidered: In Search of What Makes Us Human*. For some history of the study, try *Debating Humankind's Place in Nature, 1860–2000: The Nature of Paleoanthropology*, by Richard G. Delisle.

A *National Geographic* series, "The Dawn of Humans," covering the 6 million years of our evolution, appears in the following issues: September 1995; January and March 1996; February, May, July, and September 1997; August 1998; and May, July, and December 2000. The photographs and graphics are, as usual, superb. And see the October 2001 issue for photos of *Kenyanthropus*. A new australopithecine find is covered in the November 2006 issue and Ardi is featured in the July 2010 issue. Details of the new *Australopithecus sediba* are in the 9 September 2011 issue of *Science;* see especially "Skeletons Present an Exquisite Paleo-Puzzle" by Ann Gibbons.

For two nice popular accounts of the human evolution story, see *How Do We Know the Nature of Human Origins*, by Dale Anderson, and *The Complete Idiot's Guide to Human Prehistory*, by Robert J. Meier.

The 2 October 2009 issue of *Science* has numerous articles about Ardi. For a nice summary see "A New Kind of Ancestor: *Ardipithecus* Unveiled" by Ann Gibbons. A popular account of Ardi is in *Time* October 12, 2009, “A Long Lost Relative” by Michael D. Lemonick and Andrea Dorfman.

The latest on the effect of climate on early human evolution is “Climate and Human Evolution” by Peter B. de Menocal in the 4 February 2011 issue of *Science*.

A review of two books on the bipedalism question and a nice discussion of the topic in and of itself is Ian Tattersall’s “Stand and Deliver” in the November 2003 *Natural History*. And for more on human endurance running, see “Born to Run,” by Adam Summers, in the April 2005 *Natural History*.

The “big picture” of early hominid evolution is detailed in “The Evolutionary Context of the First Hominins” by Bernard Wood and Terry Harrison in the 17 February 2011 issue of *Nature*.

11

CHAPTER

The Evolution of Genus Homo

We carry within us the wonders we seek without us; There is all Africa and her prodigies in us.
—Sir Thomas Browne

As we saw in the last chapter, it is hard for us to agree on the fossils that represent the first 2.5 million years of the hominid record. It gets worse when we address the latest 2.5 million years. The reason is simple: this is the time during which our genus, *Homo*, evolved.

There are widely different interpretations of the nature, dates, and taxonomic affiliations of the hominid fossils from this period, and there are several divergent schools of thought regarding just what the family tree of our genus looks like. At stake in these discussions is the very identity of the species to which we all belong. In this chapter, we will address the following questions:

How can we best go about describing and organizing the fossil evidence for the evolution of genus *Homo?*

What do we know about the dates, the distribution, and the physical appearance of the various groups of fossils assigned to genus *Homo*?

What can we say about their lives, particularly about their cultural behaviors?

What is the debate over modern human origins and can it be resolved?

THE NATURE OF GENUS *HOMO*

It is fairly easy to define our genus. We have, relative to the earlier hominids, the following characteristics:

- An enlargement of the brain over the chimp-sized brains of all the earlier hominids
- Flattening of the face with a decrease in size of the teeth and jaws
- Refined bipedalism with the added ability for endurance running
- Different body proportions with relatively shorter arms
- Increasing reliance on culture as a means of adaptation
- Increasing control of and influence over the environment
- Migration eventually to all habitable areas of the planet

And yet, there is a major debate about our genus. The question is whether the groups of fossils—and, of course, recent and living modern humans—represent separate species (that is, different branches) of our genus over the last 2 million years, or whether we are all members of a single species that displays variation over time and across space. An extreme version of the first point of view proposes as many as ten different species of genus *Homo,* with *Homo sapiens* being at most 200,000 years old and profoundly different from the other species. The second extreme claims there is only one species of *Homo*—*Homo sapiens*—and that the ancient groups are regional and temporal variations within that species. Under this scheme, our species is 2 million years old. This is a huge difference! We will look more closely at this debate in the last section of this chapter.

How, then, to begin discussing the fossil evidence for the evolution of our genus if authorities cannot even agree on the names? The simplest scheme would, of course, be the one that lumps nearly all the fossils into *Homo sapiens*—that would certainly cut down on the taxonomic categories. But such an approach would make it difficult to describe and discuss differences among groups of fossils that some authorities feel are enough to merit species distinction. And when these species names are used—regardless of one's point of view on the debate—there is usually no misunderstanding about which fossils are being referred to.

Thus, let's begin with a common model that divides all later *Homo* into six species (Figure 11.1). We will describe and discuss these species

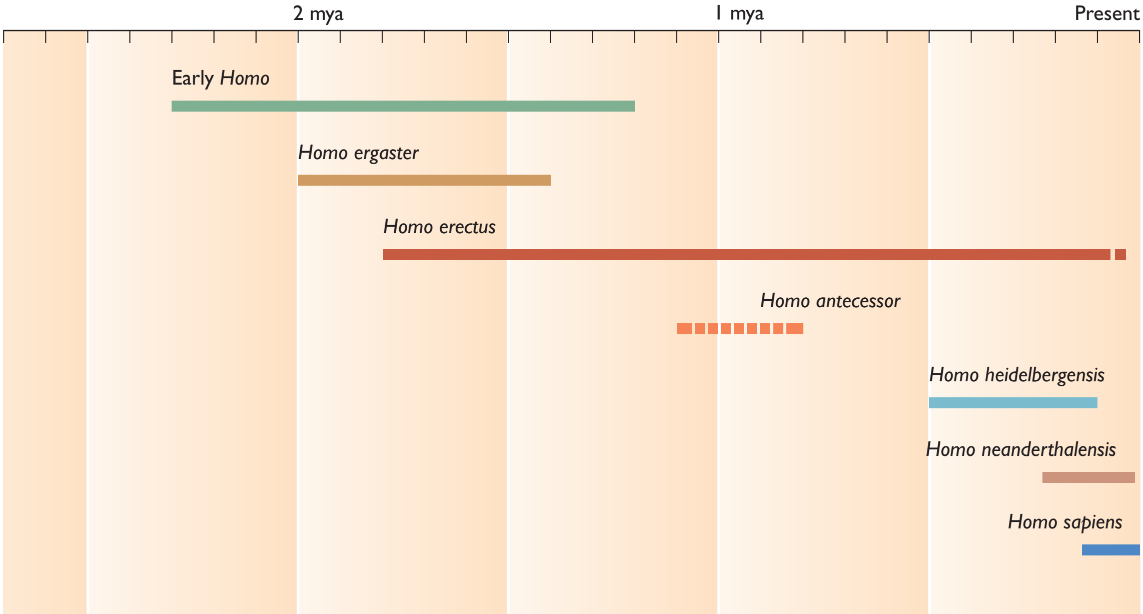


FIGURE 11.1
Timeline of species within genus *Homo* according to one model. Dashes indicate that some evidence exists for extending the time range of that species as shown. Each species, of course, may be extended in time either way as more fossil evidence is recovered. This model does not necessarily reflect the author's views but is used to clearly sort the fossils into named groups recognized by some authorities as separate species. (The so-called Hobbits from Indonesia, *Homo floresiensis,* dated at 74,000 to 12,000 ya, are still controversial and, thus, not included in this timeline. They will be discussed in the "Contemporary Reflections" box at the end of this chapter.)

in terms of their phenotypic features, dates, geographic distributions, and behaviors. Then, in the last section, we will discuss the hypotheses for just how many species these groups represent and, most important, how they are related evolutionarily. *Understand that I am not necessarily advocating this model.* I just feel that organizing our discussion in this order will allow us to easily consider both points of view.

THE FIRST MEMBERS OF GENUS *HOMO*

The First Stone Tools

When one famous fossil of *Paranthropus (P. boisei)* was found in 1959, the discoverers also found some simple stone tools at the same level of Olduvai Gorge (Figure 11.2). At first they thought *Paranthropus* had made the tools, but they began to feel that it was too primitive to have made something so sophisticated.

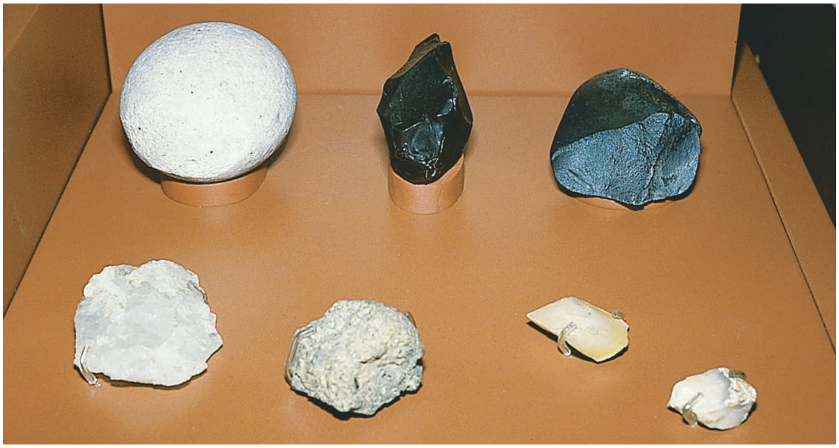


FIGURE 11.2
A sample of Oldowan tools. The two at the lower right are flake tools. The others are core tools.

Oldowan A toolmaking tradition from Africa associated with early *Homo*.

core tools Tools made by taking flakes off a stone nucleus.

flake tools Tools made from the flakes removed from a stone core.

These tools, called **Oldowan** after Olduvai Gorge (see Figure 9.7), seem very simple to us. Also called *pebble tools*, they are water-smoothed cobbles 3 to 4 inches across, modified by knocking off a few chips from one or two faces to make a sharp edge. But unlike the termite sticks of the chimpanzees, there is nothing in the raw material that immediately suggests the tools that can be made from it or the method of manufacture. A stone tool requires that the maker be able to imagine the intended tool within the stone and to picture the process needed to make it. Making even a simple Oldowan tool is a complex technological feat (Figure 11.3). (I can attest to the difficulty.) This leap of the imagination and increase in technological skill are what make the first evidence of stone toolmaking so important.

Authorities originally thought that the Oldowan tools were all **core tools** and that the flakes were the waste products of their manufacture. However, it has been shown that the majority of cores were the raw materials for the manufacture of **flake tools,** which were used for a variety of tasks, such as cutting meat and plant material, scraping meat off a bone, and sawing wood or bone (Schick and Toth 1993; Toth 1985).

It also appears that the makers of the Oldowan tools may have traveled some distance to find a source of stone known to be superior for the production of sharp, durable tools. The cores themselves were probably carried around to wherever flakes were needed; it is common to find flakes at a site but not the cores from which they were struck. All this shows a high level of planning (Schick and Toth 1993), and although there is some evidence for stone-tool manufacture among the earlier hominids, back to 3.2 mya (Braun 2010), no direct evidence of stone tools has yet been found.

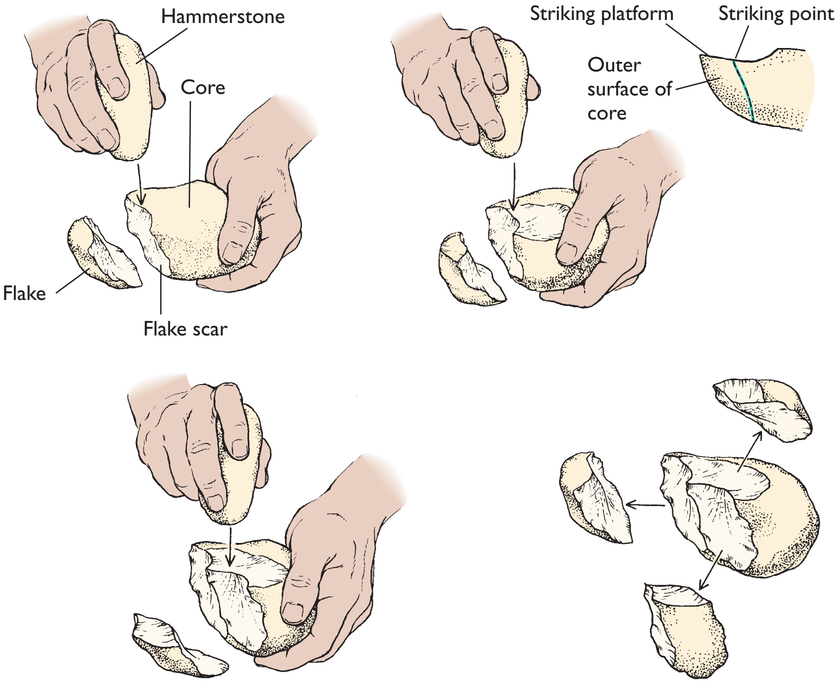


FIGURE 11.3
Process of removing flakes from a stone core in the Oldowan tradition. A hard stone was struck in just the right locations to remove sharp, thin flakes.

The Fossils

It appeared in 1959 that *Paranthropus* was not a good candidate for having been the maker of the pebble tools. Then in 1961 a second hominid from the same time period was found and named. *Homo habilis* ("handy man"; Figure 11.4).

The reasons for including these fossils in genus *Homo* were twofold. First, *H. habilis* shows a notable increase in brain size, from the average of about 480 ml for *Australopithecus* and *Paranthropus* to an average of 680 ml, with a possible maximum of 800 ml. Second, the presence of the stone tools indicates that those larger brains were capable of a complexity of thought not seen before. Subsequent finds showed a postcranial skeleton more intermediate between *Homo* and *Australopithecus*, but with the indications of features related to endurance running. Thus, *H. habilis* seems to mark the beginning of a new trend in hominid evolution—toward bigger brains and greater intelligence and changes in bipedalism. Fossils of *H. habilis* have now been found in Tanzania, Kenya, Ethiopia, and perhaps southern Africa and have been dated at 2.3 to 1.44 mya.

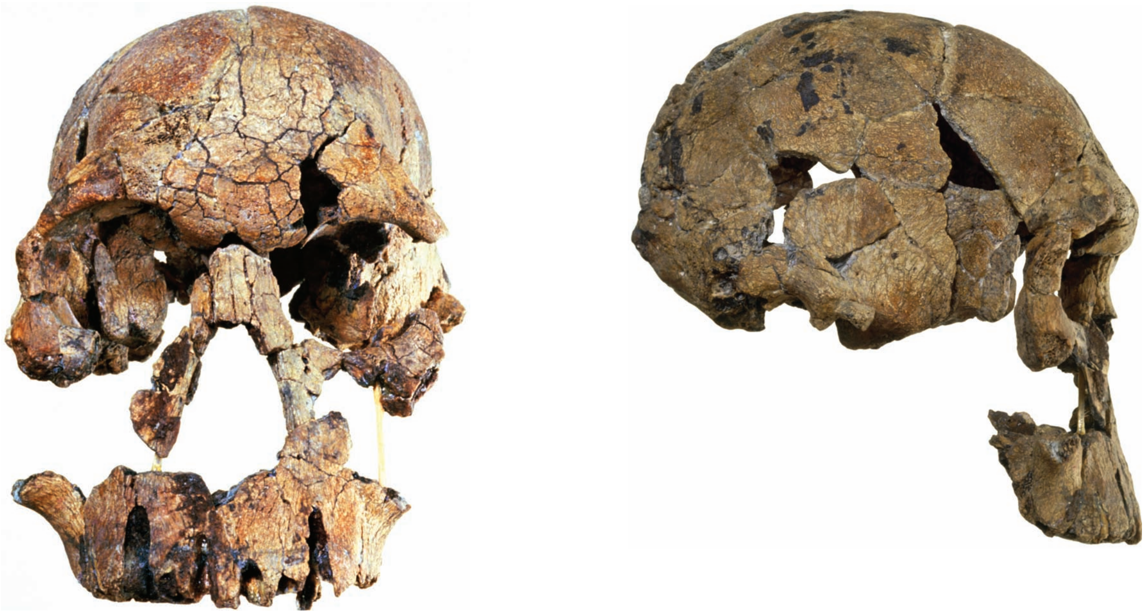


FIGURE 11.4
The well-known skull 1470 from Lake Turkana, Kenya, front and side views. Note the flatter face, smoother contours, lack of a sagittal crest, and more rounded braincase as compared with *Australopithecus* and *Paranthropus*. This fossil was first classified as *Homo habilis* and still is by some authorities. Others consider it a separate species, *Homo rudolfensis*.

The exact taxonomic affiliations of this group of fossils, however, are far from agreed upon. The specimens from East Turkana, Kenya, are considered different enough by some to be placed in a new species, *Homo rudolfensis*. Others believe that all these specimens belong in *H. habilis*. Still others feel that the fossils labeled *H. habilis* and *H. rudolfensis* are in important ways closer to *Australopithecus* than to *Homo* and should thus be lumped into the former genus. Still others agree that while *H. habilis* might be lumped into *Australopithecus*, *H. rudolfensis* should remain in *Homo*. (See Tattersall 1992, Wood and Collard 1999, and Gibbons 2011b for more detail on this debate.) For the remainder of this discussion, we will use the term "early *Homo*," in keeping with what is, at the moment, the majority view, and we will consider all the fossils together. As more fossils that cover a broader span of time are found, the picture of hominid evolution during this period should become clearer.

A New Adaptive Mode

What is it about the stone tools that may have given early *Homo* an edge? Paleoanthropologist Richard Leakey suggests that sharp stone tools allowed these hominids to more quickly cut meat and bones off a carcass, making the addition of meat to the diet through scavenging safer and more efficient. There is evidence for this suggestion.

Ten sites from the early *Homo* period contain Oldowan tools, flakes, and animal bones. These are "stone cache" sites (Potts 1984) where hominids left supplies of stones and to which they took scavenged animal remains for quick, safe processing and eating. Analysis indicates that these sites were used for short periods, but repeatedly, as one would expect of such places.

Archaeologist Lewis Binford (1985) has analyzed the animal bones from these sites and found that they are mostly the lower leg bones of antelopes. These bones carry little meat and, along with the skull, are about the only parts left after carnivores and scavengers have finished eating. However, such bones are rich in marrow, so a major activity at the sites in question may have been to cut off what little meat remained on these bones and then to break them open for the nutritious marrow inside.

Finally, Pat Shipman has studied the taphonomy of these and other bones with a scanning electron microscope (1984, 1986). She found that cut marks left by stone tools were usually on the shafts of the bones as if pieces of meat were cut off, not near the joints as if an entire carcass had been butchered (Figure 11.5). The hominid tool marks sometimes overlapped carnivore tooth marks, showing that the carnivores had gotten there first.

We may envision early *Homo* in small cooperative groups, maybe family groups, foraging in a mixed grassland/woodland area for plant foods and always on the lookout for the telltale signs of a carnivore kill—a group of scavengers gathered on the ground or a flock of vultures circling overhead. Their big brains allowed them to better understand their environment and

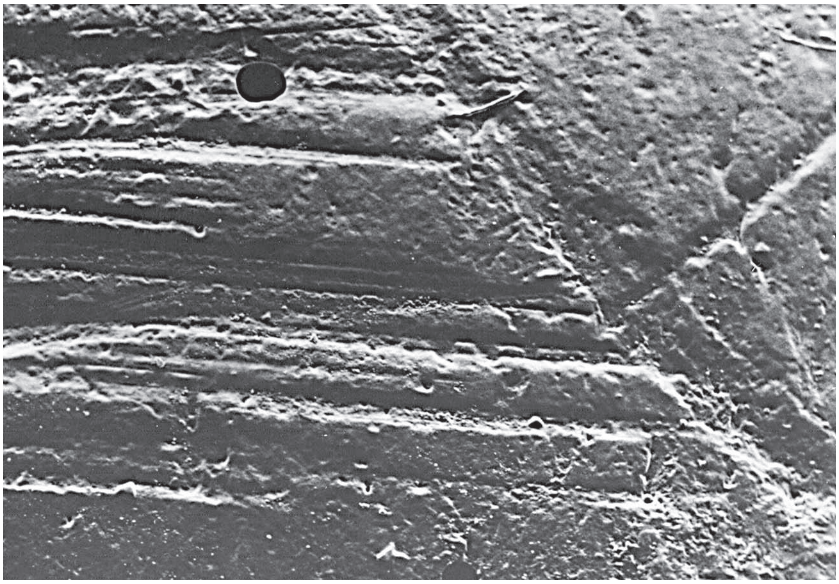


FIGURE 11.5
This micrograph of a fossil bone from Olduvai Gorge shows tool marks (the horizontal lines and the diagonal line beginning at the top of the photo) and a carnivore tooth mark (beginning on the right side and angled toward the center). In this case, the tooth mark overlaps the tool mark, indicating that the hominids sliced meat off this part of the bone *before* a scavenger began eating.

to manipulate it, making imaginative and technologically advanced tools from stone. With these tools they may have cut apart the carcasses they found and taken the pieces back to a safe place where they had stored more tools. There they cut the remaining meat off the bones and, using large hammerstones, smashed open the bones for marrow. It was no doubt a harsh life, but it was successful. The adaptive themes of bipedalism, large brains, social organization, and tool technology set the stage for the rest of hominid evolution.

Fossils indicate that forms with the characteristics of early *Homo* were around for about 2 million years. Before they disappeared from the fossil record, a new hominid species came on the scene—one that continued and enhanced the trends of big brains and tool technology, adaptations that soon carried this hominid all over the Old World.

TO NEW LANDS

The First Fossils

Most of the fossils at the beginning of genus *Homo* (subsequent to the still-debated fossils of early *Homo*) are undisputed members of our genus and are included in species *Homo erectus*. Some authorities split the African fossils of this group into a second species, *Homo ergaster* (Table 11.1 and Figure 11.6).

TABLE 11.1
Major Fossils of *Homo ergaster* and *Homo erectus*

Country	*Locality*	*Fossils*	*Age (million years)*	*Est. Brain Size (ml)*
Homo ergaster				
Kenya	East Turkana	Cranial and postcranial fragments including mandibles and pelvis and long bone fragments	1.78 1.57	850 800
		Cranial fragments	1.55	691
	West Turkana	Nearly complete juvenile individual	1.6	880
Homo erectus				
Algeria	Ternifine	3 mandibles and a skull	0.5–0.7	—

(continued)

TABLE 11.1 (Continued)

Country	*Locality*	*Fossils*	*Age (million years)*	*Est. Brain Size (ml)*
Homo erectus (continued)				
China	Hexian (Lontandong)	Partial skull	0.25–0.5	1,000
	Lantian (Gongwangling)	Cranial fragments and mandible	>1	800
	Longgupo	Mandible fragments	1.8	—
	Yunxian	2 crania	>0.35	—
	Zhoukoudian	Cranial and postcranial remains	0.77	1,030
		of 40 individuals	0.77	915
			0.77	850
			0.77	1,225
			0.77	1,015
			0.77	1,030
			0.77	—
	Tangshan Cave	Fragments	0.58–0.62	—
Ethiopia	Bouri	Cranial and postcranial fragments	1.0	995
Georgia	Dmanisi	3 mandibles,	1.77	780
		16 teeth,	1.77	650
		3 crania, postcranial bones	1.77	600
Israel	‘Ubeidiya	Fragments	<1	—
Italy	Ceprano	Cranium	0.8–0.9	—
Java	Modjokerto	Child’s cranium	1.8	—
	Ngandong	Cranial and postcranial fragments	<0.1	1,170
		from >12 individuals	<0.1	1,250
			<0.1	1,230
			<0.1	1,090
	Sambungmachan	Large cranial fragment	<0.1	1,000
	Sangiran	Cranial and postcranial fragments	1.6	800
		from ~40 individuals	1.6	900
			1.6	850
			1.6	1,050
			1.6	1,000
			1.1–1.4	856
	Trinil	Skullcap and femur	<1	940
Kenya	Olorgesailie	Cranial fragments	0.90–0.97	<800
	Ileret	Cranial fragment	1.55	—
Morocco	Salé	Cranium	0.4	880
	Sidi Abderrahman	2 mandible fragments	—	—
	Thomas Quarry			
		Mandible and skull fragments	0.5	—
Tanzania	Olduvai	Cranial and postcranial fragments,	1.4	1,060
		including mandibles and pelvis and	0.6–0.8	700–800
		long bone fragments		
Turkey	Kocabaş	Cranial fragments	0.51–0.49	—
			Mean	**984.79**

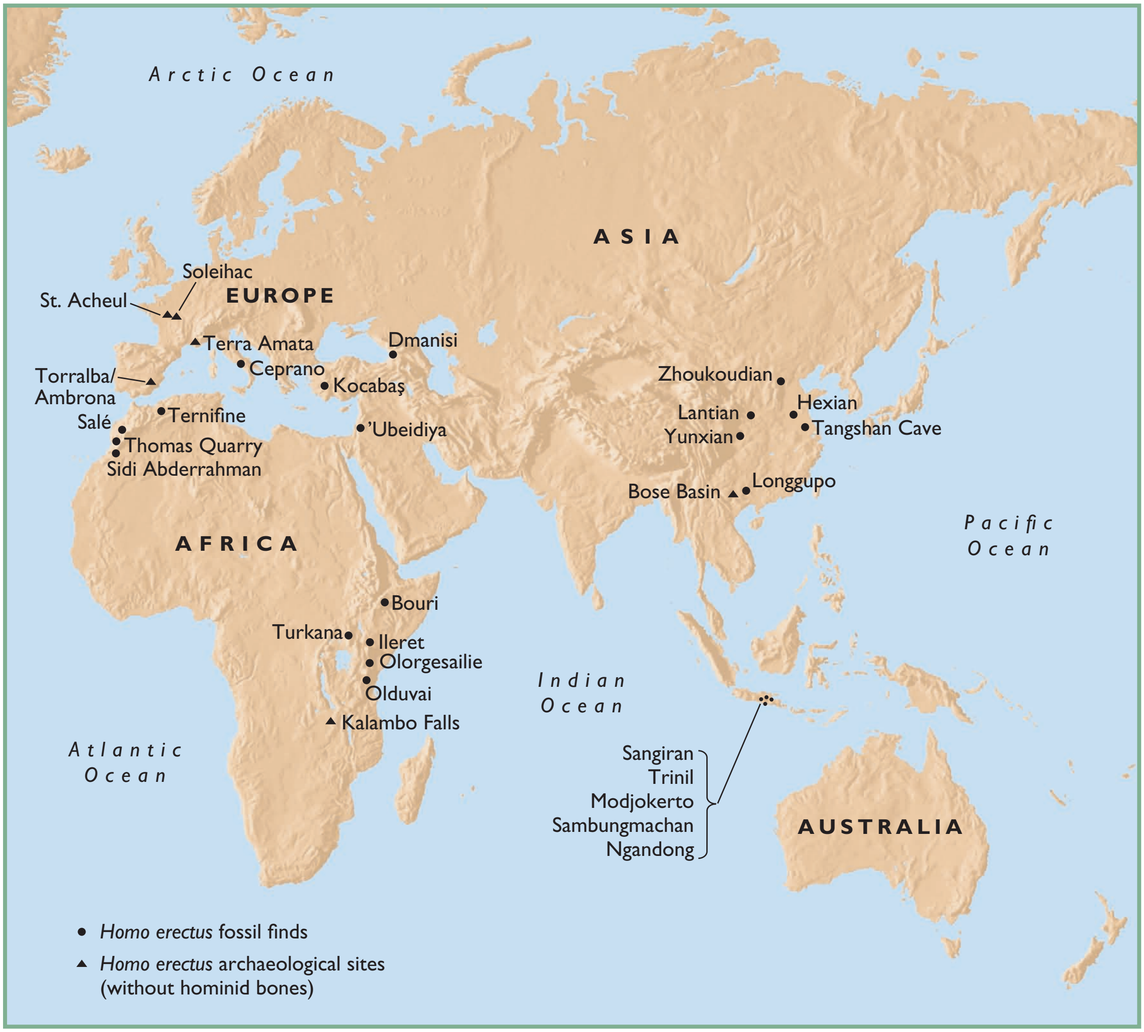

Arctic Ocean
ASIA
Soleihac
St. Acheul
EUROPE
Terra Amata
Dmanisi
Ceprano
Kocabaş
Torralba/
Ambrona
Salé
Ternifine
'Ubeidiya
Thomas Quarry
Sidi Abderrahman
Zhoukoudian
Lantian
Yunxian
Hexian
Tangshan Cave
Bose Basin
Longgupo
Pacific
Ocean
AFRICA
Bouri
Turkana
Ileret
Olorgesailie
Olduvai
Kalambo Falls
Indian
Ocean
Atlantic
Ocean
Sangiran
Trinil
Modjokerto
Sambungmachan
Ngandong
AUSTRALIA
● *Homo erectus* fossil finds
▲ *Homo erectus* archaeological sites
(without hominid bones)

FIGURE 11.6
Map of major *Homo erectus*/*ergaster* sites.

The Dutch physician Eugene Dubois made the first finds of *H. erectus* in Java in 1891. Dubois chose Java to look for hominid fossils largely because he was already stationed there with the military. But the choice was also a logical one for the time, since most people thought that humans had first evolved in Asia, despite Darwin's clear suggestion that Africa was the human homeland. The idea that our

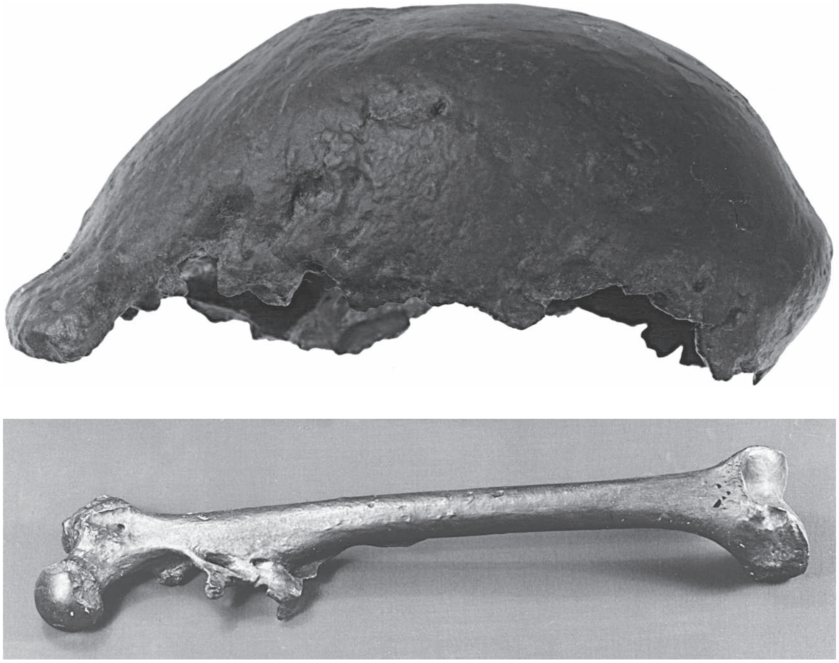


FIGURE 11.7
Skullcap and femur of "Java Man" *Homo erectus*. The growth near the neck of the femur is the result of a pathological condition.

evolutionary line was originally African apparently did not sit well with many Europeans.

When Dubois found a skullcap and a diseased femur at the site of Trinil (Figure 11.7), he thought they represented the "missing link" between apes and humans, and he dubbed the specimens "Pithecanthropus erectus" (the "upright ape-man"), popularly known as "Java Man." Since Dubois's work, numerous other fossils have been located in Java (see Table 11.1) and are now recognized as fully hominid and assigned to our genus, *Homo*.

Perhaps the most famous *H. erectus* fossils are those from Zhoukoudian, a cave outside of Beijing, China. Starting in the 1920s, six nearly complete skulls, a couple dozen cranial and mandible fragments, over a hundred teeth, and a few postcranial pieces were recovered from the cave. Stone tools and animal bones, including those of horses and hyenas, were also recovered. The hominid remains are clearly similar to other specimens of *H. erectus*. Dating indicates that the cave was first occupied about 770,000 ya and was used until about 230,000 ya, although new evidence

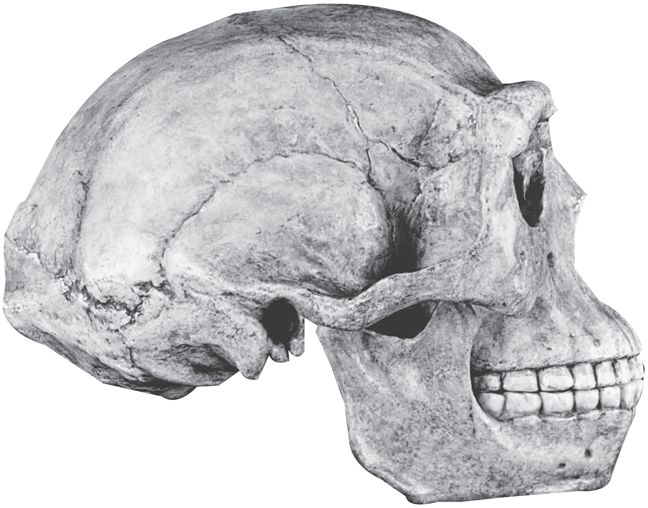


FIGURE 11.8
Cast of one of the missing "Peking Man" skulls.

(Boaz and Ciochon 2001) suggests that most of the *H. erectus* bones in the cave were the remains of hyenas' meals.

The fame of the Zhoukoudian fossils, called "Peking Man" (from the old spelling of Beijing), lies mostly in the fact that they are missing. When Japan invaded China in 1937, U.S. Marines attempting to get the fossils out of the country were captured by Japanese troops. The fossils were never seen again. Their whereabouts remain one of the great mysteries in anthropology. Fortunately, extensive measurements had already been taken of the bones, and accurate casts had been made (Figure 11.8).

Since then, numerous fossils classified as *H. erectus* have been recovered, and we are filling in our knowledge of this important period in hominid evolution. Among the oldest fossils of this group are those that some authorities place in a separate species, *H. ergaster* ("work man," a reference to stone tools found in association with the fossils). The oldest well-established find, from East Turkana in Kenya, is dated at 1.78 mya (Figure 11.9). In some ways it is typical of *H. erectus* crania. It has heavy brow ridges, a prognathous face, a sloping forehead, an elongated profile, a **sagittal keel,** a sharply angled occipital bone with a pronounced **torus,** and a cranial capacity of 850 ml (Figure 11.10). (The sagittal keel should not be confused with the sagittal crest. The crest is a ridge of bone for the attachment of chewing muscles [see Figure 10.14]. The keel is an aspect of the skull's shape.) The average cranial capacity for this hominid

sagittal keel A sloping of the sides of the skull toward the top, as viewed from the front.

torus A bony ridge at the back of the skull, where the neck muscles attach.

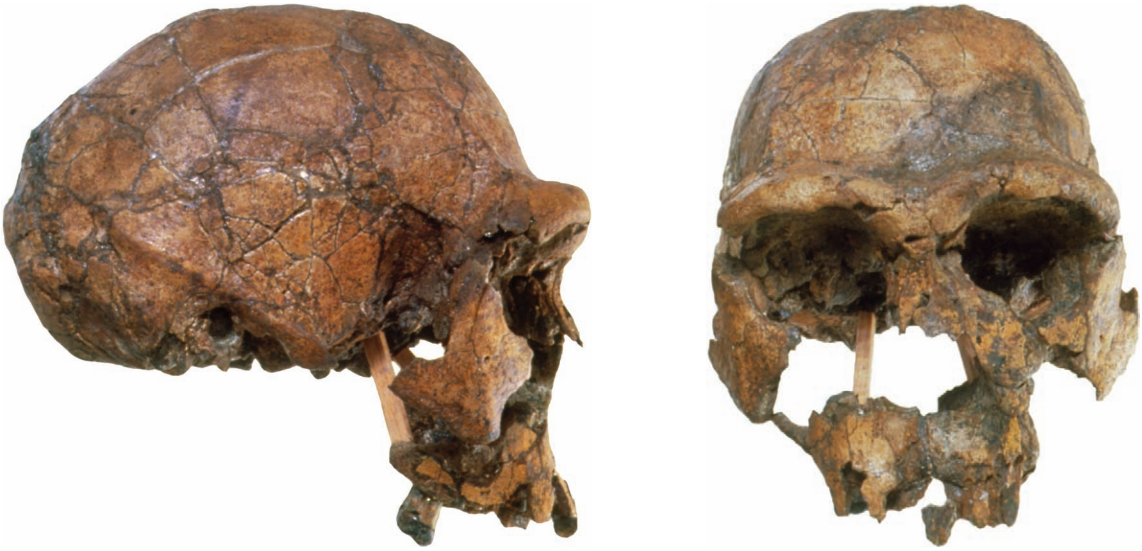


FIGURE 11.9
The *Homo erectus* (or *Homo ergaster*) skull of KNM-ER 3733 from Lake Turkana, Kenya, is fairly typical of this group.

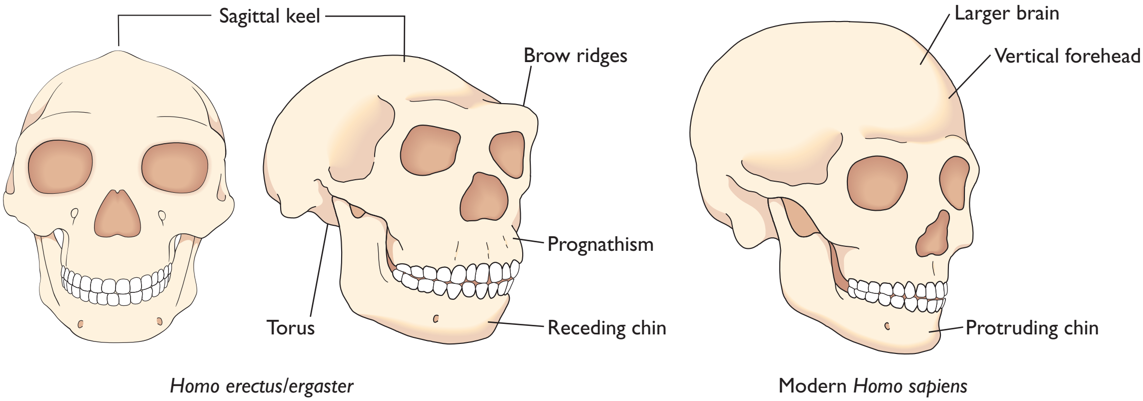

Sagittal keel
Brow ridges
Prognathism
Torus
Receding chin
Homo erectus/ergaster
Larger brain
Vertical forehead
Protruding chin
Modern *Homo sapiens*

FIGURE 11.10
Cranial features of *Homo erectus/ergaster* (side and front views) compared with those of modern *Homo sapiens.*

group is about 980 ml, just slightly under the modern human minimum of 1,000 ml, but a considerable jump from the 680 ml average for early *Homo*. Some *H. erectus* fossils have cranial capacities within the modern human range (see Table 11.1).

In other ways, however, the Turkana skull differs from others labeled as *H. erectus*, which has led to its placement in *H. ergaster*.

From the neck up, then, *H. erectus/ergaster* is quite distinct from early *Homo* in overall size, ruggedness, and especially brain size. The skull still retains primitive features that distinguish it from modern *H. sapiens*. From the neck down, however, *H. erectus/ergaster* is essentially modern and apparently was so from its beginnings.

We know this because one of the oldest fossils of the group—also included in *H. ergaster*—is also the most complete. It is a nearly whole skeleton found at West Turkana in Kenya and is dated at 1.6 mya (Figure 11.11). The shape of the pelvis indicates that it was a male. Based on dental eruption and lack of any epiphyseal union, it is estimated that he was 12 years old when he died. "Turkana Boy," as he is commonly known, was about 5½ feet tall; he might have been 150 pounds and 6 feet tall had he lived to adulthood. *H. erectus/ergaster* spread throughout the African continent and populations of the group remained there for about a million years.

Migration and the Ice Ages

H. erectus, however, did not remain only in Africa. Members of the species had reached West Asia, China, and Southeast Asia by almost 2 mya. What prompted them to leave the savannas to which they were apparently so well adapted?

Why They Left A good guess is that the spread of *H. erectus* was simply an outcome of their reproductive success. Their big brains enabled them to exploit the savannas to a greater extent than had the other hominids to date. They had better and more varied tools (which we'll discuss later), the ability to learn more about their environment and to reason out the problems that their habitat presented, and, no doubt, a more complex social organization. With these adaptations, *H. erectus* would have rapidly increased in population size.

Population increase, however, puts pressure on resources and, perhaps, on social harmony. So groups of *H. erectus* probably split and moved outside of familiar areas in search of less competition over food, space, and two other resources that may have been even more important on the savannas—water and shelter. They may also have been following migrations of animal herds that had become important sources of food.

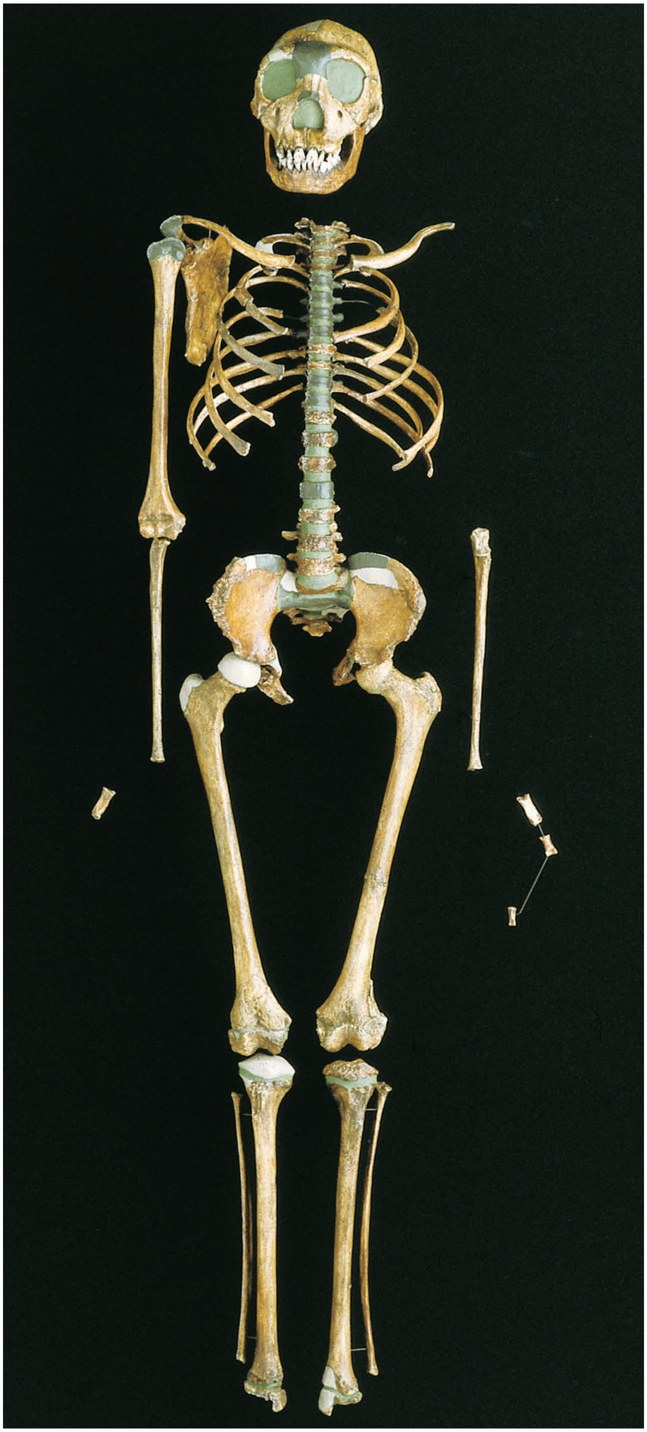


FIGURE 11.11
The "Turkana Boy," *Homo ergaster* fossil KNM-WT 15000, is one of the most complete early hominid fossils ever found. The pelvis is clearly that of a male, and the epiphyses at the top of his left femur are obviously not fused (see Figure 9.3).

The Pleistocene In search of these resources, *H. erectus* wandered the Old World. At first, their travels would have been made easier because, at the time, the savannas stretched from western Africa, across southern Asia, and all the way to northern China. Those wanderings eventually carried them as far from their African homeland as what is now Beijing, China, and the Indonesian island of Java, and perhaps to Europe. Not only did these journeys take them to new climates, but the travels also brought them into contact with the changeable environments of the ice ages, known technically as the **Pleistocene.**

Beginning about 1.6 mya and ending 10,000 ya, the Pleistocene was a complex series of extremely cold periods separated by warm phases, some warmer than today. There may have been as many as eighteen cold episodes during the Pleistocene, some lasting tens of thousands of years. We still don't know what caused these cold periods. Suggestions range from increased volcanic activity, with dust and ash blocking the sun's rays, to changes in the earth's orbit.

When the average world temperature drops, ice and snow accumulate over the years at the poles and in higher elevations. The pressure of this accumulation forces the movement of great sheets and rivers of ice known as **glaciers** (Figure 11.12). During periods of glacial advances, much of North America, Europe, and Asia were covered by ice, sometimes nearly a mile thick (Figure 11.13). Parts of the world not covered by the glaciers were also affected, having cooler summers and wetter winters. The advance of the glaciers also had the effect of condensing the world's climatic zones into smaller spaces. Several times during the Pleistocene, the temperate oak and pine forests of Connecticut, where I now live, were like the arctic **tundra** of Alaska and northern Canada. Moreover, with so much of the earth's water tied up in the great ice sheets, sea levels dropped as much as 400 feet, exposing large areas of land formerly under water. This allowed humans to migrate to areas previously inaccessible; this is how modern *Homo sapiens* migrated to North America.

Dating the Migrations When did *Homo erectus* leave Africa and when did they arrive at other locations where their fossils have been found?

The latest dating of some *H. erectus* fossils and dates of some newer finds pose an interesting problem. *Homo erectus* shows up all over the Old World, as far away as Java, in a very short time—just a few hundred thousand years or less—after they first appear in Africa. This could mean that *H. erectus* evolved somewhere other than Africa. But all previous hominid fossils come only from Africa, so it's unlikely that *erectus* evolved anywhere but there.

Pleistocene The geological time period, from 1.6 mya to 10,000 ya, characterized by a series of glacial advances and retreats.

glaciers Massive sheets of ice that expand and move.

tundra A treeless area with low-growing vegetation and permanently frozen ground.

FIGURE 11.12
A veritable river of ice, the Moreno Glacier is located in Patagonia, a region of Argentina.

That leaves two plausible explanations. Perhaps *H. erectus* (or *ergaster*) first evolved in Africa earlier than any of the fossils we have—remember how rare fossilization is—and then spread. The other possibility is simply that their expansion began very shortly after they first evolved and was rapid. Science writer James Shreeve (1994:86) notes that Java is 10,000

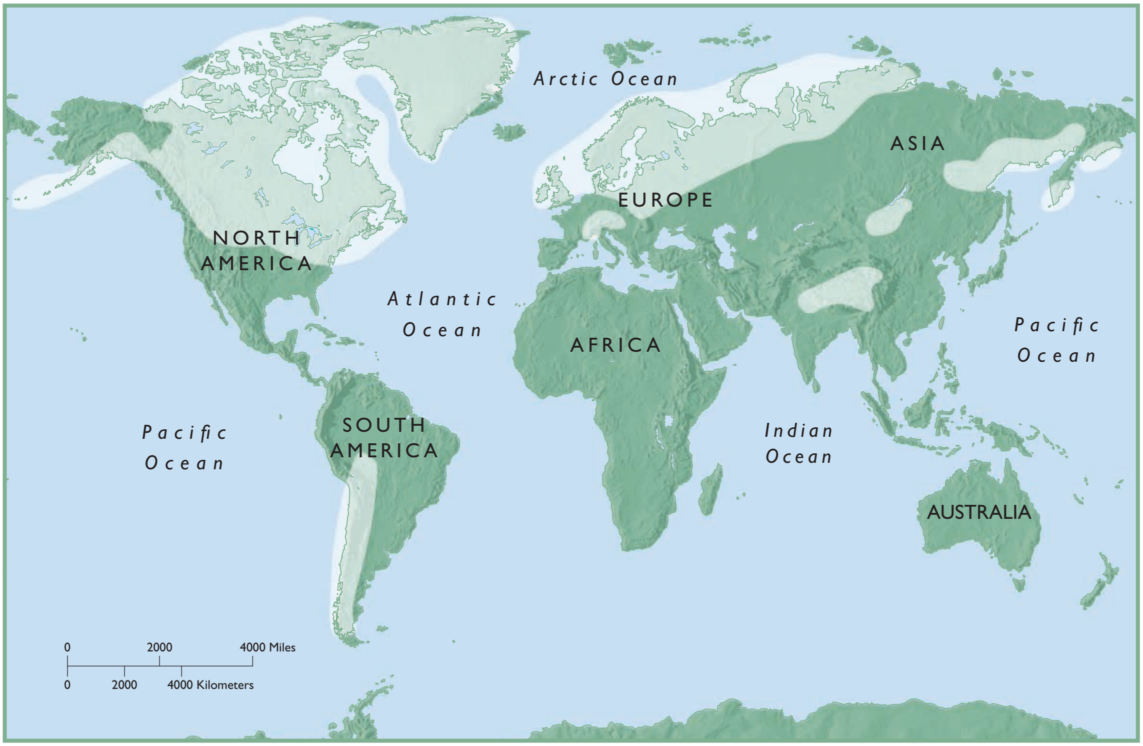

Arctic Ocean
ASIA
EUROPE
NORTH AMERICA
Atlantic Ocean
AFRICA
Pacific Ocean
Pacific Ocean
SOUTH AMERICA
Indian Ocean
AUSTRALIA
0
2000
4000 Miles
0
2000
4000 Kilometers

FIGURE 11.13 Maximum worldwide glacial expansion during the Pleistocene. The Antarctic ice cover, not shown here, also expanded during this epoch.

to 15,000 miles from Africa, depending on the route, and that parts of Indonesia were connected to Asia at the time due to lower sea levels during the Pleistocene. If *erectus* walked just a mile a year, it would have taken only about 15,000 years to reach Java. That's still pretty fast, considering that they did not necessarily move 1 mile every year *in the right direction*. I think that if the currently accepted dates are correct (see Table 11.1), they probably mean that *H. erectus/ergaster* is both older than we now assume based on existing fossils *and* that the species' expansion began early on.

Evidence for this idea comes from the Dmanisi site in the Republic of Georgia. The hominid crania from this site were dated at 1.77 mya and assigned to *Homo erectus* (Figure 11.14). A newer find in 2002, of the same age, was distinct, however, in being smaller and having some features resembling early *Homo*, in other words, it appears to be a transitional form. One interpretation, then, is that hominids may have ventured out of Africa sooner and at an earlier evolutionary stage than we had thought (Balter and Gibbons 2002; Dennell and Roebroeks 2005). Even new fossils from the site, postcranial bones found in 2007, also show a mix of traits, among the more "primitive" traits some shoulder and arm features, short stature (4 feet

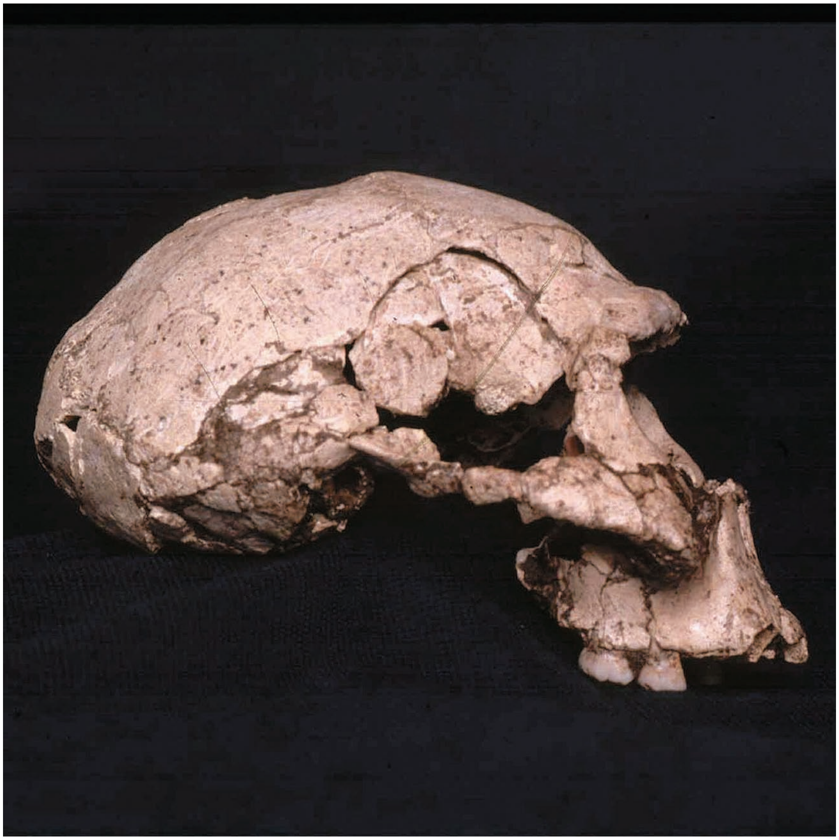


FIGURE 11.14
One of the previously discovered crania from Dmanisi, Georgia, dated 1.77 mya and provisionally assigned to *Homo erectus*. The skulls from this site show a remarkable degree of variation, and some have traits that resemble early *Homo* from Africa.

9 inches to 5 feet 5 inches) and small body mass (88 to 110 pounds), much smaller than "Turkana Boy," who lived at about the same time.

There is also a skull found in Kenya, dated 1.55 mya, that displays intermediate features like the Dmanisi cranium, and some stone tools from China dated at 1.36 mya. It appears, then, as if, indeed, hominids left Africa almost as soon as the basic theme of our genus, *Homo*, was established.

At the other end of the range of *Homo erectus*, there is evidence from Java that members of this species may be younger than 100,000 years—perhaps as young as 27,000 to 53,000 years old. If so, there were populations of *erectus* still around well after modern *Homo sapiens* had evolved. (We'll discuss the meanings of this in the last section of the chapter.)

It should be noted that with the exception of the Ceprano find in Italy (see Table 11.1), the European evidence of *H. erectus* comes in the form of cultural artifacts dated to times that have been associated with that species from other locations. At the site of Soleihac in France are tools and animal

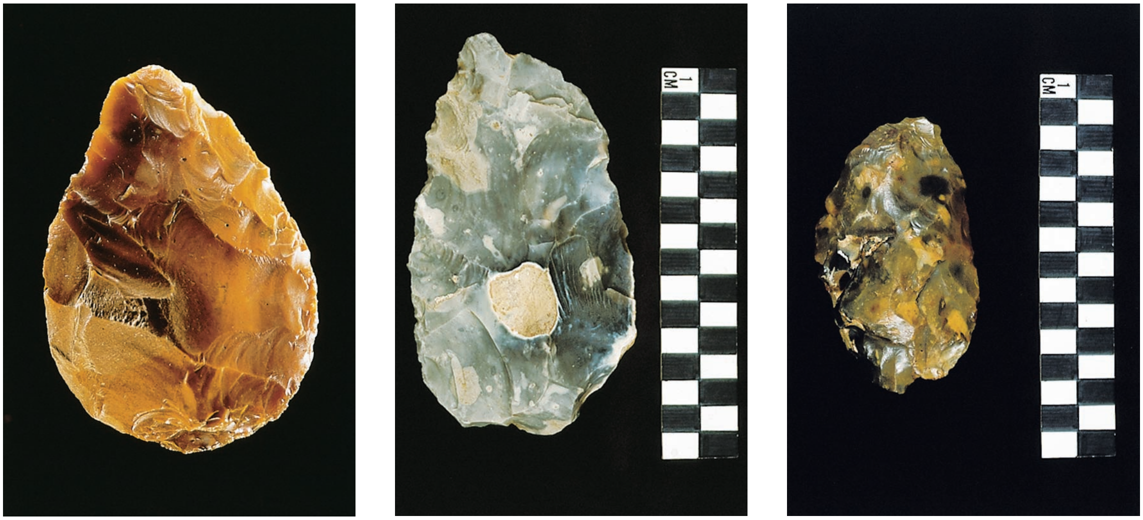


FIGURE 11.15 Bifacially flaked hand axes became one of history's most popular tools and were found in a variety of sizes showing varying degrees of quality. The hand axe on the far right is from the French site of St. Acheul, which lent its name to this toolmaking tradition.

remains dated at 800,000 ya. Another French site, Terra Amata, on the Riviera, has been proposed as a site where *H. erectus* built shelters around 400,000 ya. In Spain, at two adjacent sites called Torralba and Ambrona, dated at 400,000 ya, are the remains of some large mammals, including elephants, along with some stone tools that suggest a hunting or, more probably, a scavenging site. Until, however, we locate definite fossils of *H. erectus* from Europe—other than the cranium from Ceprano, Italy—we can only conclude that the species was there but was not widespread or, perhaps, that these sites are associated with another hominid species.

The Life of *Homo erectus*

Acheulian technique A toolmaking tradition associated with *Homo erectus* in Africa and Europe.

hand axe A bifacial, all-purpose stone tool, shaped somewhat like an axe head.

bifacial Refers to a stone tool that has been worked on both sides.

Tools Like early *Homo*, early *H. ergaster* made stone tools by taking a few flakes off a core, just enough to make the "business end." They also, of course, used the flakes as tools. But beginning about 1.76 mya, *H. erectus* elaborated on this stone toolmaking technique by flaking the entire stone, controlling the shape of the whole core tool. This toolmaking tradition is called the **Acheulian technique,** after the site in France where it was first identified. The core tool produced by the Acheulian technique is the **hand axe.** It is symmetrical, edged and pointed, and **bifacial** (flaked on both sides; Figure 11.15). It was the all-purpose tool of its time, used for any number of tasks, from butchering to cutting wood.

In addition to hand axes, *H. erectus* also made tools with straight, sharp edges called *cleavers*. Moreover, making a hand axe or cleaver produces

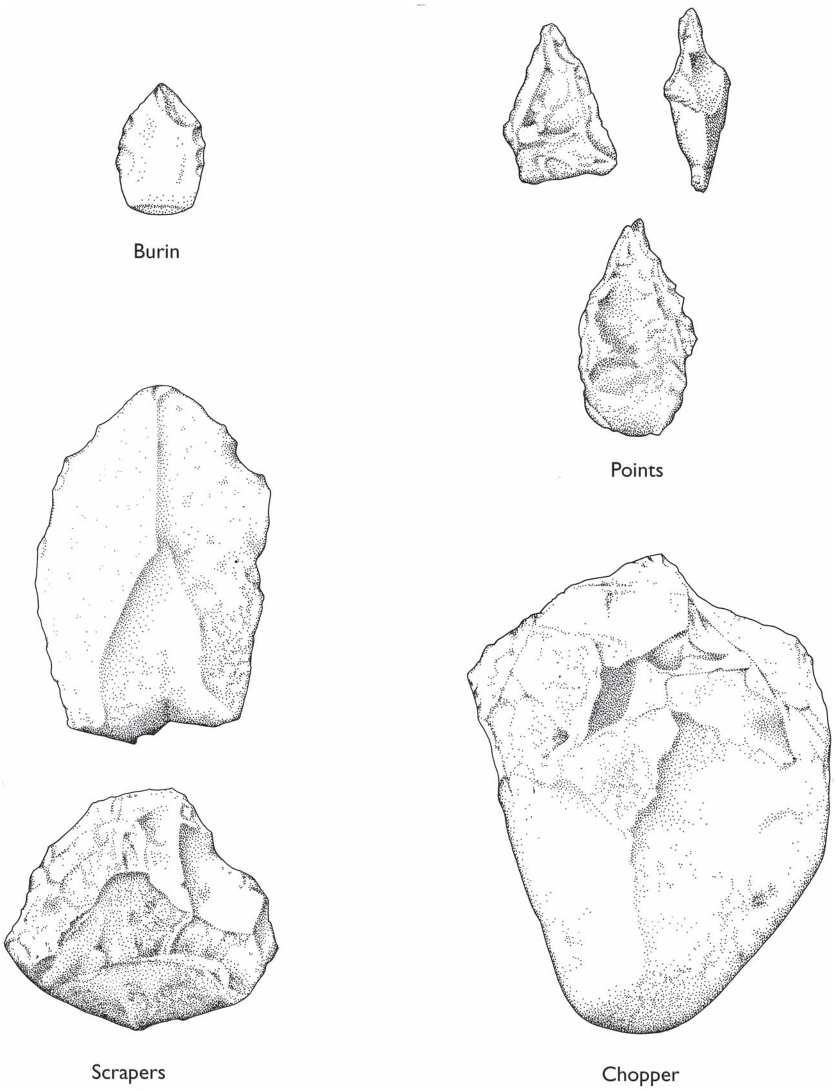


FIGURE 11.16
Flake and chopper tools associated with *Homo erectus* from the cave at Zhoukoudian. Although the functions of these tools are uncertain, some are named for inferred use. Burins may have been used to etch out thin slivers of antler or bone, which were then further modified into awls or needles. Points may have served as cutting tools for fine work. Scrapers may have helped remove flesh from animal hides. And choppers chopped wood and perhaps broke open bones to extract marrow.

a great many flakes—as many as fifty usable ones by one estimate—used either unmodified or further worked to produce a desired shape.

Hand axes appeared in Africa about 1.76 mya and lasted for over a million years. They spread throughout Africa and into Europe. They are, however, rarely found in Asia. Instead, Asian *erectus* populations made *choppers*, with flakes removed from one or both sides (Figure 11.16) but asymmetrical and not flaked over the whole surface.

Fire Perhaps the most striking behavioral advance associated with *Homo erectus* is the purposeful use of fire. There is some evidence, though it is disputed, for the use of fire in Africa at 1.5 mya and France at 750,000 ya. A rock shelter in Thailand has yielded evidence of fire dated at 700,000 ya. The earliest well-accepted date (although even it is not without its skeptics) is from the cave at Zhoukoudian sometime after 500,000 ya (Binford and Chuan 1985; Binford and Stone 1986).

Fire, of course, provides heat, and so it is not surprising that some of the earliest evidence of fire comes from cold northern areas. Fire also provides protection from animals and can be used for cooking, making meat easier to chew and digest. (It should be noted that all evidence points to *Homo erectus* still being scavengers and not yet big-game hunters.) But in the long run, perhaps its most important use is as a source of light. Science writer John Pfeiffer (1966) suggests that fire could extend the hours of activity into the night and provide a social focus for group interaction. Sitting around the campfire at night was when people experimented, created, talked, and socialized. Fire serves these functions in human cultures today. Moreover, the use of fire may well have given people a psychological advantage—a sense of mastery and control over a force of nature—and a source of energy. As Pfeiffer says in the title of his article, "When *Homo erectus* Tamed Fire, He Tamed Himself."

Language What about the linguistic skills of *H. erectus*? Their average cranial capacity was just a little short of the modern human minimum, and individual *erectus* remains fall within the modern human range. It's difficult to be certain what this fact means. After all, the modern range of 1,000 to 2,000 ml means that some people have brains twice the volume of others, but there is no solid evidence that within this range brain size has anything to do with intelligence. Was *H. erectus*, then, just a little bit less intelligent than we are?

Because the inside of the skull reflects some of the features of the brain it once held, anthropologist Ralph Holloway (1980, 1981) has been able to look at the structure of *H. erectus* brains. By making **endocasts** of the inside surfaces of fossil crania, Holloway has produced images of the very brains of our ancestors (Figure 11.17). One intriguing find is that the brains of *H. erectus* were asymmetrical—the right and left halves of the brain weren't the same shape. This is found to some extent in apes but to a greater extent in modern humans, because the halves of our brains perform different functions. Language and the ability to use symbols, for example, are functions of the left hemisphere, while spatial reasoning (such as the hand-eye coordination needed to make complex tools) is performed in

endocasts Natural or human-made casts of the inside of a skull.

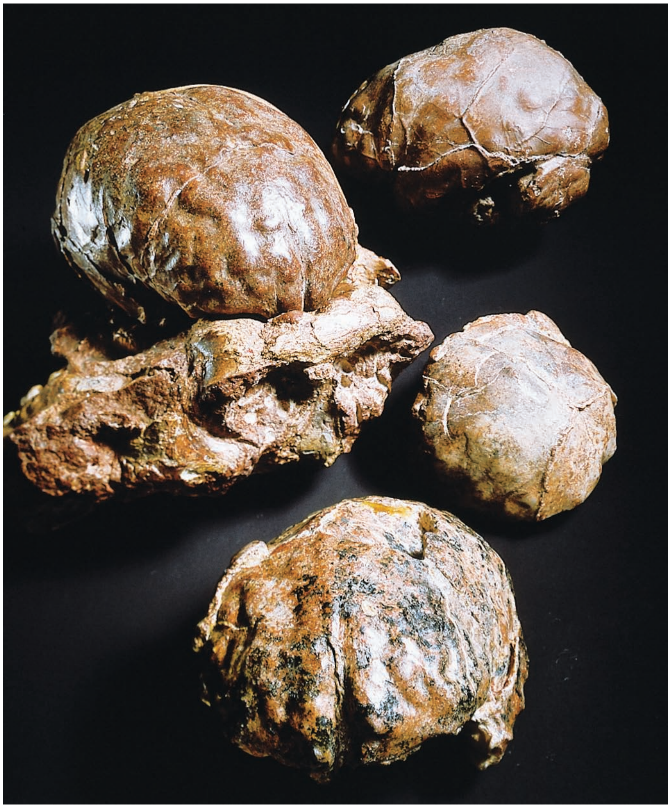


FIGURE 11.17 Natural endocasts from South African australopithecines. Notice the degree of detail, particularly the blood vessels of the upper right cast. Such casts may also be made artificially and allow us to compare the brains of our ancestors with those of modern humans.

the right hemisphere. This hints that *H. erectus* also had hemisphere specialization, perhaps even including the ability to communicate through a symbolic language.

Further evidence of language use by *H. erectus* is suggested by the reconstruction of the vocal apparatus based on the anatomy of the cranial base. Even though the vocal apparatus is made up of soft parts, those parts are connected to bone, and so the shape of the bone is correlated with the shape of the larynx, pharynx, and other features (Figure 11.18).

Reconstruction work on australopithecines indicates that their vocal tract was basically like that of apes, with the larynx and pharynx high up in the throat. While this would have allowed them to drink and breathe at the same time (as human infants can do up to 18 months), it would not have allowed for the precise manipulation of air that is required for modern human languages. The early hominids could make sounds, but they would have been more like those of chimpanzees.

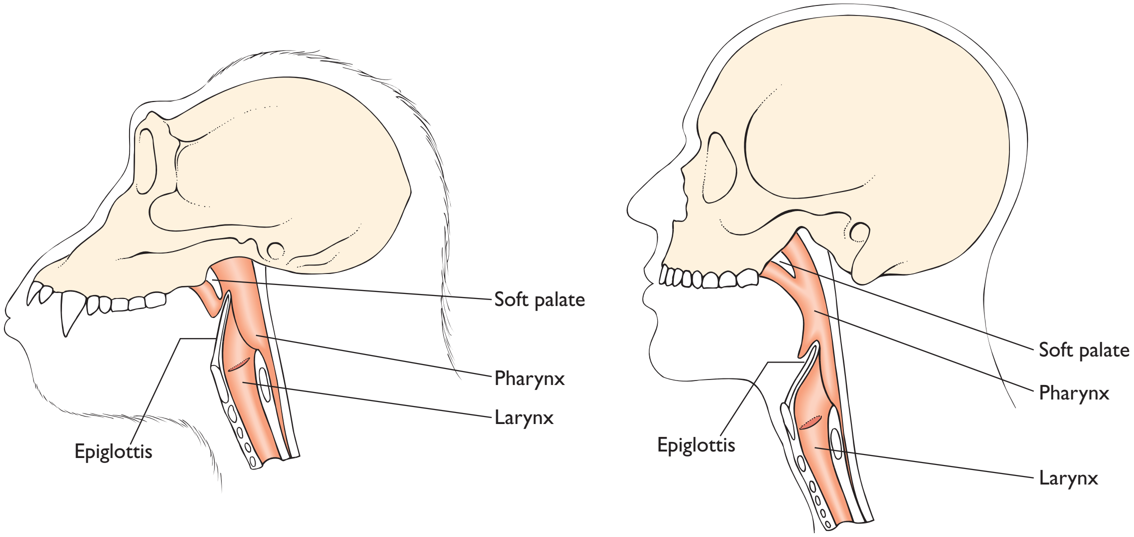


FIGURE 11.18
Vocal tract of a chimp compared with a modern human's. The high placement of the chimp's vocal tract makes it impossible for it to produce all of the sounds that are part of modern human languages.

Homo erectus, on the other hand, had vocal tracts more like those of modern humans, positioned lower in the throat and allowing for a greater range and speed of sound production. Thus, *erectus* could have produced vocal communication that involved many sounds with precise differences. Whether or not they did so is another question. But given their ability to manufacture fairly complex tools, to control fire, and to survive in different and changing environmental circumstances, *erectus* certainly had complex things to talk *about*. It is not out of the question that *erectus* had a communication system that was itself complex, although there are authorities who feel that a communication system with the attributes of modern human language is associated only with the sophisticated behavior of modern *Homo sapiens* (see Holden 1998 for a detailed discussion).

If we can consider it a separate species, *H. erectus*—although now extinct—was a smashing success by any standards. The species evolved nearly 2 mya in Africa, possibly from an earlier species, *H. ergaster*, and by perhaps 1.8 mya had spread as far as Java. By 500,000 ya, they had reached northern China and Europe. They lasted as an identifiable group in Africa and China until 250,000 ya and may have persisted in Java until less than 100,000 ya. Their adaptations—now focused on learning, technology, and the cultural transmission of information—allowed them to exploit a number of different environments.

There is some debate over just how much *H. erectus* changed during their tenure on earth. There is a small increase in average cranial capacity over this time (about 180 ml), as well as some refinement in their hand axe–making technique and variation in their flake tool production. These changes, however, are small and slow, so the overall impression is one of stability—not a bad thing in evolutionary terms.

As early as 800,000 ya, and perhaps earlier there was another sudden surge in brain size, to an average matching our own. This marks the beginning of perhaps the most complex part of our story.

BIG BRAINS, ARCHAIC SKULLS

The next three hominid species—using the six-species model, illustrated in Figure 11.1—are marked by brain sizes within the modern human range that match or approximate the modern human average; nonetheless, they have other features, especially of the cranium, that retain primitive characteristics. These hominid groups are sometimes collectively referred to as "archaic." The most recent of these, *Homo neanderthalensis*, will be considered separately in the next section. Here we will discuss the earlier *H. heidelbergensis* and the even earlier *H. antecessor* (Table 11.2 and Figure 11.19).

Homo antecessor

The newest suggested hominid species, named in mid-1997, is *Homo antecessor* ("advance guard" or "explorer"). Many authorities do not recognize the fossils involved as a separate species, but the discoverers see sufficient distinctions to warrant the new name (Bermúdez de Castro et al. 1997). Fossils have been discovered at two sites in the Atapuerca Hills in northern Spain. They consist of more than eighty fragments, including skulls, jaws, teeth, and other portions, as well as tools and animal bones. Gran Dolina, the first site found, is dated at more than 780,000 ya, and the most recent site, Sima del Elefante (Carbonell et al. 2008), is dated at 1.2 to 1.1 mya. Assuming these dates are correct, these would be the oldest well-accepted hominid fossils in Europe. Analysis of the cranial specimens estimates the brain size at more than 1,000 ml.

TABLE 11.2
Major Fossils of *Homo antecessor* and *Homo heidelbergensis*

Country	*Locality*	*Fossils*	*Age (years)*	*Est. Brain Size (ml)*
Homo antecessor				
Spain	Gran Dolina	More than 80 fragments	>780,000	>1,000
	Sima del Elefante	Mandible	1,100,000–1,200,000	—
Homo heidelbergensis				
China	Dali	Cranium	200,000	1,120
	Jinniushan(?)*	Nearly complete skeleton	200,000	1,350
	Maba(?)	Cranium	130,000–170,000	—
	Xujiayao(?)	Fragments of 11 individuals	100,000–125,000	—
England	Swanscombe	Occipital and parietals	276,000–426,000	1,325
	Boxgrove†	Tibia, teeth	362,000–423,000	—
Ethiopia	Bodo	Cranium	600,000(?)	1,250
France	Arago	Cranium and fragmentary remains of 7 individuals	250,000	1,200
Germany	Bilzingsleben(?)	Cranial fragments and tooth	320,000–412,000	—
	Mauer	Mandible	500,000	—
	Steinheim(?)	Cranium	200,000–240,000	1,200
Greece	Petralona	Cranium	160,000–240,000	1,200
Hungary	Vértesszöllös	Occipital fragment	250,000–475,000	1,250
India	Narmada	Cranium	200,000	1,300
Spain	Sima de los Huesos	2,500 fragments from at least 33 individuals	300,000	1,390
Tanzania	Ndutu (Olduvai)(?)	Cranium	400,000–700,000	1,100
Zambia	Kabwe (Broken Hill)	Cranium and additional cranial and postcranial remains of several individuals	400,000–700,000	1,280
			Mean	**1,247.00**

*The (?) indicates that the species identification of that fossil is in question.

† Some flint tools have recently been discovered at the site of Pakefield in southeast England. They are dated at 700,000 ya, but no fossil remains indicate that a hominid species is responsible for them (Parfitt et al. 2005).

The most striking fossil is the partial face of an 11-year-old boy (Figure 11.20). His features, described by the researchers as "fully modern," include a projecting nose region with a sharp lower margin, hollowed cheekbones, and several details of the dentition.

On the other hand, other fossils from this site show primitive features such as prominent brow ridges and premolars with multiple roots (modern

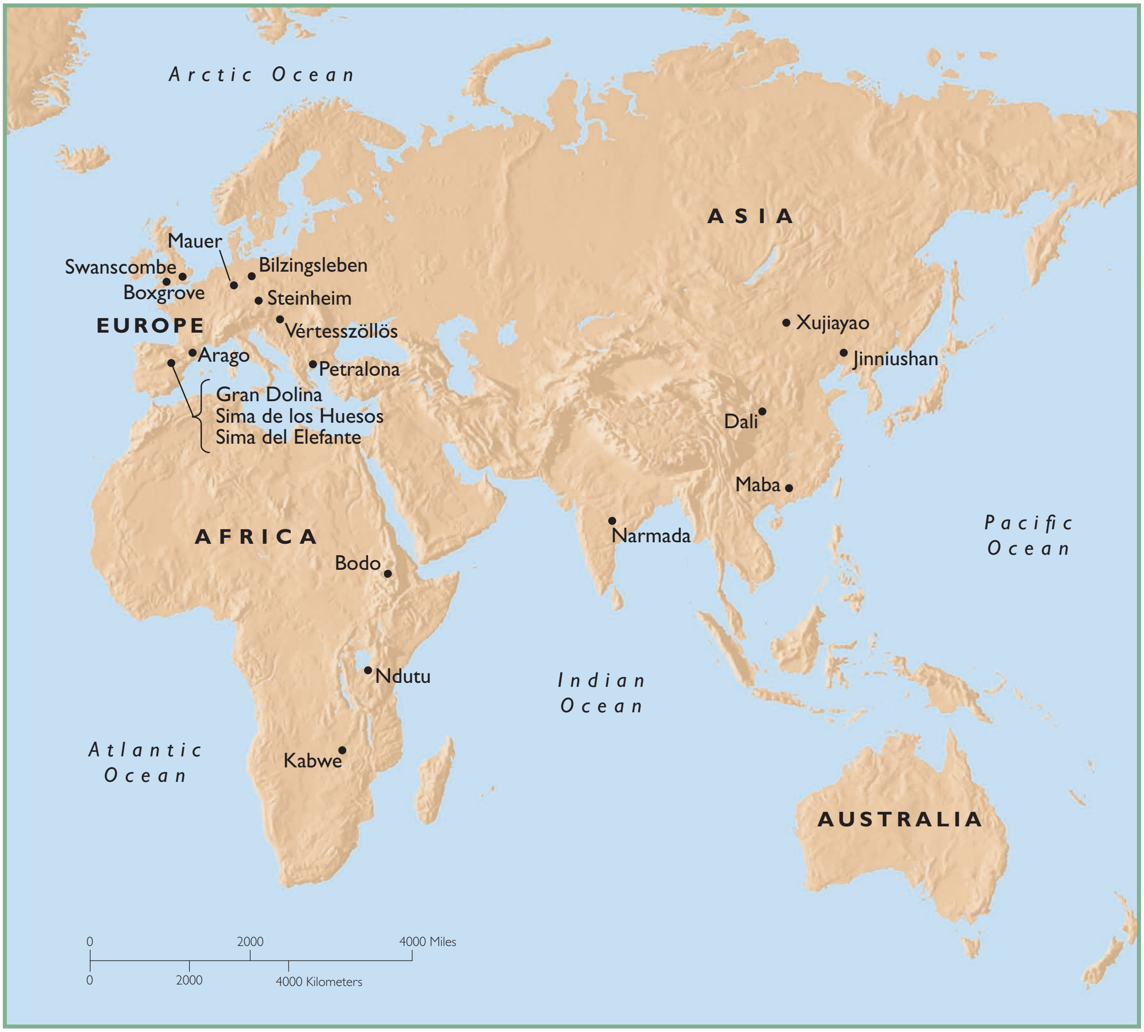

Arctic Ocean
ASIA
Mauer
Swanscombe
Bilzingsleben
Boxgrove
Steinheim
EUROPE
Vértesszöllös
Arago
Petralona
Gran Dolina
Sima de los Huesos
Sima del Elefante
Xujiayao
Jinniushan
Dali
Maba
AFRICA
Narmada
Bodo
Pacific Ocean
Ndutu
Indian Ocean
Atlantic Ocean
Kabwe
AUSTRALIA
0
2000
4000 Miles
0
2000
4000 Kilometers

FIGURE 11.19 Map of major *Homo antecessor* and *Homo heidelbergensis* sites.

human premolars have a single root). This unique mix of traits, especially the very modern appearance of the face, is what led the investigators to assign the new species name—and to further suggest that this species is the direct ancestor both of modern humans and of *H. heidelbergensis* and *H. neanderthalensis*.

The earliest-dated tools found at Gran Dolina resemble pre–hand axe tools from Africa, cores and simple cutting flakes. Later tools are more sophisticated. One long flake has a sharp edge on one side and a dulled flat

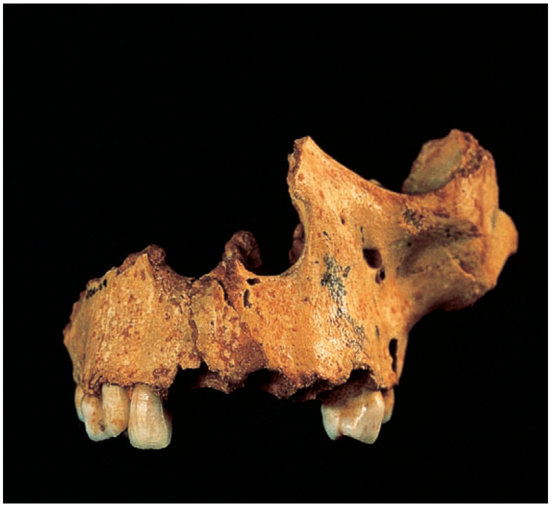


FIGURE 11.20
Fossil ATD6-69 from Gran Dolina cave, Atapuerca, Spain. This partial face of an 11-year-old boy who died perhaps more than 780,000 ya is fully modern in many features, including the hollowed cheekbone easily seen here.

edge on the other. It was presumably used as a knife. None of the tools at the sites, however, are as complex as some of the Acheulian tools being made by *H. erectus* and *H. ergaster* at the same time period or earlier.

Bison and deer bones, as well as some from other species, have been found that show stone-tool cut marks. Whether this implies hunting or scavenging is unclear. According to the investigators, there are also cut marks on some of the human bones that were mixed in with animal bones, suggesting cannibalism (Kunzig 1997).

Homo heidelbergensis

Table 11.2 and Figure 11.19 show that the fossils assigned to *Homo heidelbergensis* are geographically widespread and range over about 275,000 years in time. The species was first named for a mandible found in 1907 at Mauer, near Heidelberg, Germany.

Members of this group show an average brain size of nearly 1,300 ml, a more than 30 percent increase over the average for *H. erectus*. The brains are also differently proportioned than those of *H. erectus*, with greater emphasis on the forebrain, reflected by steeper foreheads. This may be important because the frontal lobes of the human brain are the areas thought to be most involved in the control of voluntary movements, speech, attention, social behavior, planning, and reasoning (see Figure 7.5).

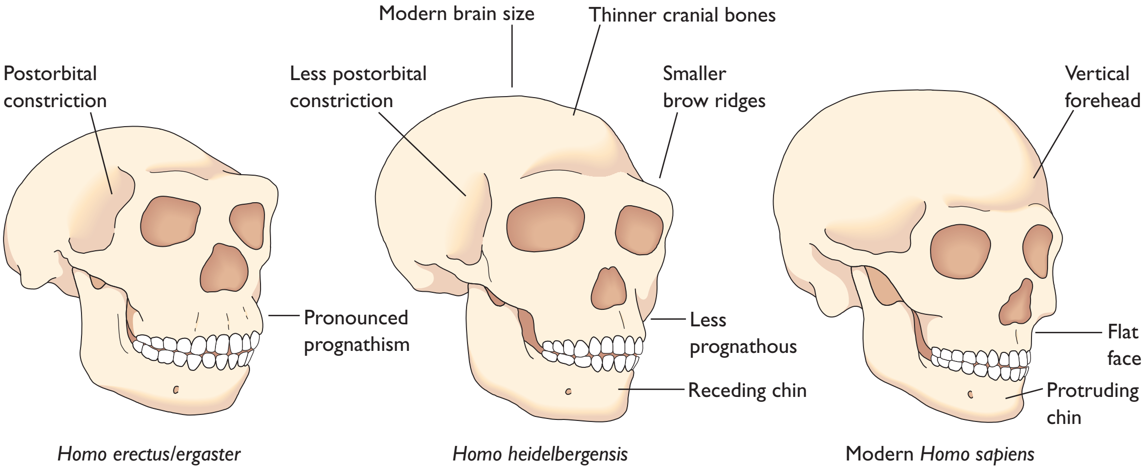

Postorbital constriction
Pronounced prognathism
Homo erectus/ergaster
Modern brain size
Thinner cranial bones
Less postorbital constriction
Smaller brow ridges
Less prognathous
Receding chin
Homo heidelbergensis
Vertical forehead
Flat face
Protruding chin
Modern Homo sapiens

FIGURE 11.21
Cranial features of *Homo erectus/ergaster, Homo heidelbergensis,* and modern *Homo sapiens.*

The bones of the cranium, compared with those of *H. erectus*, are thinner; the overall size of the face is reduced; the profile is less prognathous; the brow ridges, though still present, are less pronounced; and the **postorbital constriction,** characteristic of *erectus*, is lessened (Figure 11.21). The postcranial skeletons, essentially modern in overall shape, are more rugged and muscular than in modern humans. Figures 11.22 and 11.23 show two of the more complete examples of *H. heidelbergensis* crania.

By about 200,000 ya, people included in *H. heidelbergensis* invented a new and imaginative way to make stone tools. The method appears first in Africa and later in Europe. Called the *prepared core*, or **Levallois technique** (after the suburb of Paris where it was first recognized), it involved the careful preparation of the rough stone core so that up to four or five flakes of a desired shape could be taken off. The flakes could then be used for cutting, scraping, or piercing. Figure 11.24 shows the steps involved and a replica of such a tool. There is also evidence of other materials used for manufacturing tools, such as some wooden spears from the 400,000-year-old site of Schöningen in Germany. The size and characteristics of these approximately 6-foot-long weapons suggest that they were meant to be thrown at fairly large animals (Thieme 1997).

Finally, an intriguing but still dim glimpse into the lives of the people of this era comes from another site in Atapuerca, Spain, near Gran Dolina (Kunzig 1997). Known as Sima de los Huesos ("pit of bones"), it is a shaft inside a cave containing at least thirty-three humans—many so well preserved that they include even fingertips and small inner ear bones. Most of the bones are from teenagers and young adults, both male and female. Although the

postorbital constriction A narrowing of the skull behind the eyes, as viewed from above.

Levallois technique A tool technology involving striking uniform flakes from a prepared core.

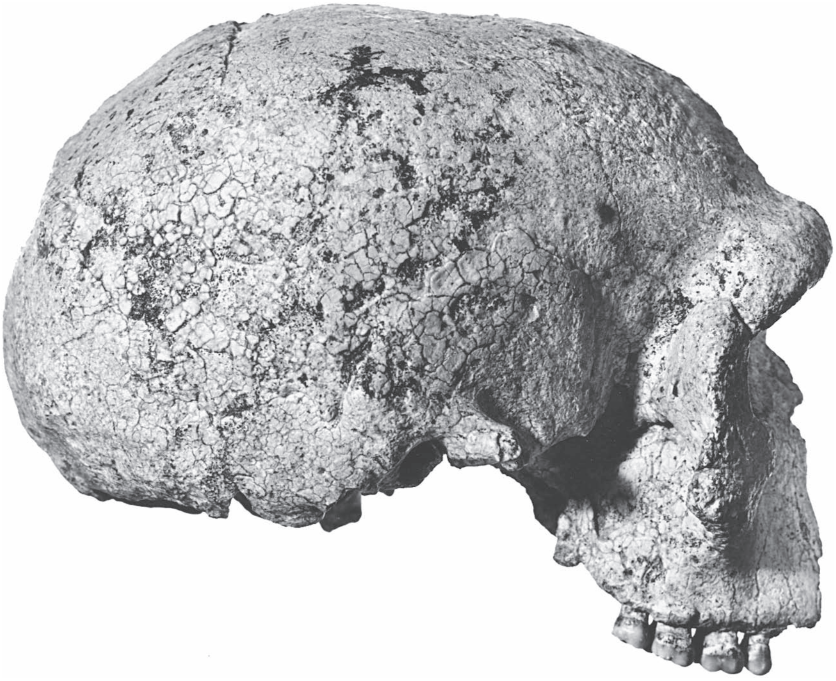


FIGURE 11.22
Skull of *Homo heidelbergensis* from Steinheim, Germany. Note the more rounded shape and higher forehead as compared with *H. erectus*. At the same time, note the retention of heavy brow ridges.

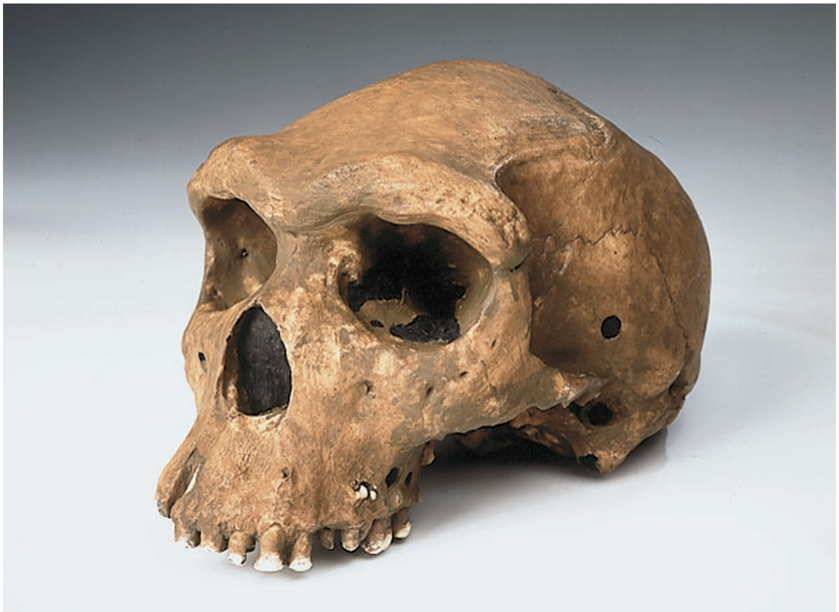


FIGURE 11.23
The Kabwe (formerly called Broken Hill) specimen is one of the best-known examples of a premodern *Homo sapiens* from Africa. Note the extremely large brow ridges on this skull, which has a cranial capacity of 1,280 ml, quite close to the modern average.

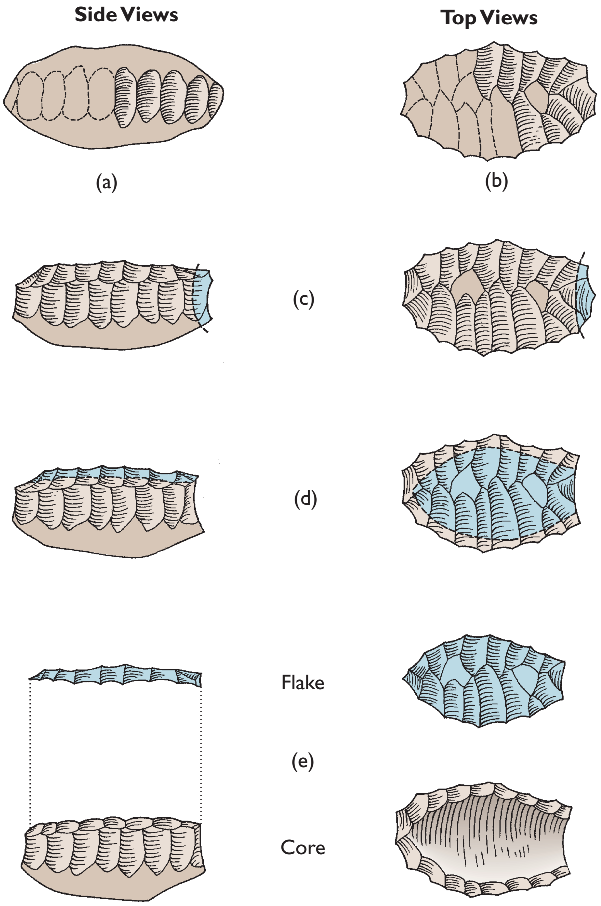

Side Views
Top Views
(a)
(b)
(c)
(d)
Flake
(e)
Core

FIGURE 11.24
The Levallois technique step-by-step: (*a*) produce a margin along the edge of the core, (*b*) shape the surface of the core, (*c, d*) prepare the surface to be struck (the “striking platform”), (*e*) remove the flake, and return to step (*b*) for additional flake removal. Shown below is a replica of a Levallois core and tool.

bones show signs of chewing by a carnivore, it is unlikely that some predator would have selected just that age group, and the nonhuman remains in the pit are not those of prey animals but those of foxes and bears, which may have fallen in and chewed on the human bones before dying. Investigators think the bodies were thrown into the pit after death (one seems to have died from a massive infection), probably not as part of a formal funeral ritual (no artifacts were found) but more likely for simple disposal purposes. Perhaps they all died together in some catastrophe. Many of the bones show signs of childhood malnourishment.

No doubt the peoples labeled *H. antecessor* and *H. heidelbergensis* had other mental, cultural, and perhaps physical adaptations to help them deal with the various and changeable environments they encountered as the Pleistocene continued. We certainly know this was true for one famous group of humans from Europe and the Near East. Some crania from Sima de los Huesos are said to show traits that might be ancestral to this next group, the Neandertals.

THE NEANDERTALS

The Neandertals—*Homo neanderthalensis* in the six-species model—were named after one of the first human fossils found and recognized as a human fossil, a skullcap from the Neander Valley in Germany recovered in 1856 (Figure 11.25). This was before Darwin wrote *Origin of Species*. (In

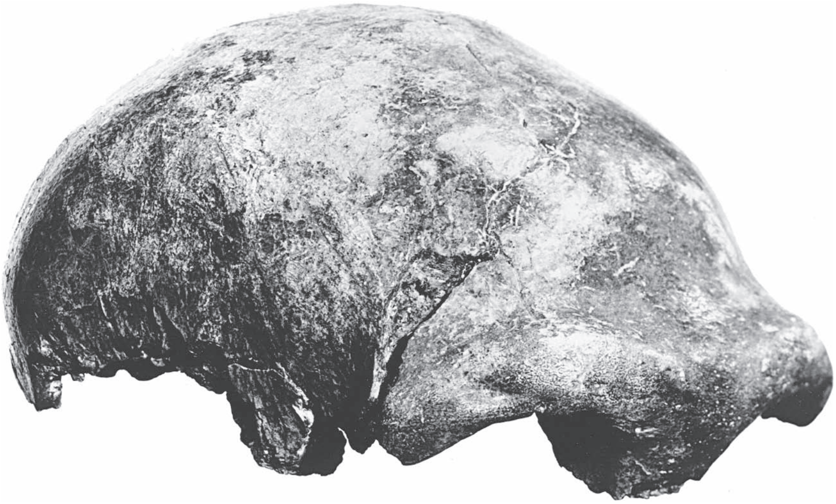


FIGURE 11.25
The original Neandertal skullcap from Germany. The cranial vault held a very large brain, but the brow ridges indicate an obvious difference from modern humans.

TABLE 11.3
Major Fossils of *Homo neanderthalensis*

Country	*Locality*	*Fossils*	*Age (years)*	*Est. Brain Size (ml)*
Belgium	Spy	2 skeletons	—	—
Croatia	Krapina	Cranial and postcranial fragments of >45 individuals	130,000	1,200–1,450
	Vindija	52 fossil fragments	28,000–42,000	—
France	Biache St. Vaast	2 crania	150,000–175,000	—
	Fontechévade	Cranial fragments of several individuals	100,000	1,500
	La Chaise	Cranium	126,000	—
	La Chapelle-aux-Saints	Skeleton	—	1,620
	La Ferrassie	8 skeletons	>38,000	1,680
	St. Césaire	Skeleton	36,000	—
Germany	Neandertal	Skullcap	—	>1,250
	Ehringsdorf	Cranial fragment	225,000	—
Gibraltar	Forbe's Quarry	Cranium	50,000	—
Iraq	Shanidar	9 partial skeletons	70,000	1,600
Israel	Amud	Skeleton	70,000	1,740
	Kebara Cave	Postcranial skeleton	60,000	—
	Tabun	Skeleton, mandible, postcranial fragments	100,000	1,270
Italy	Monte Circeo	Cranium	—	—
	Saccopastore	Cranium	—	—
Russia	Byzovaya (?)	Tools only	32,000	—
	Mezmaiskaya	Infant skeleton	36,000–73,000	—
Uzbekistan	Teshik-Tash	Child's cranium and partial skeleton	70,000	—
			Mean	**1,478.89**

German, *thal* means "valley" and is always pronounced *tal*. Recent spelling drops the silent *h*, but some still use it. The formal species name retains its original spelling.) Table 11.3 and Figure 11.26 show the basic data for fossils of this species and the locations of these finds.

The Neandertals have had an interesting history in anthropology. At one time they were considered brutish, hunched-over, dim-witted members of a dead-end side branch of human evolution. At other times they have been thought of as an ancient, different-looking form of *Homo sapiens*

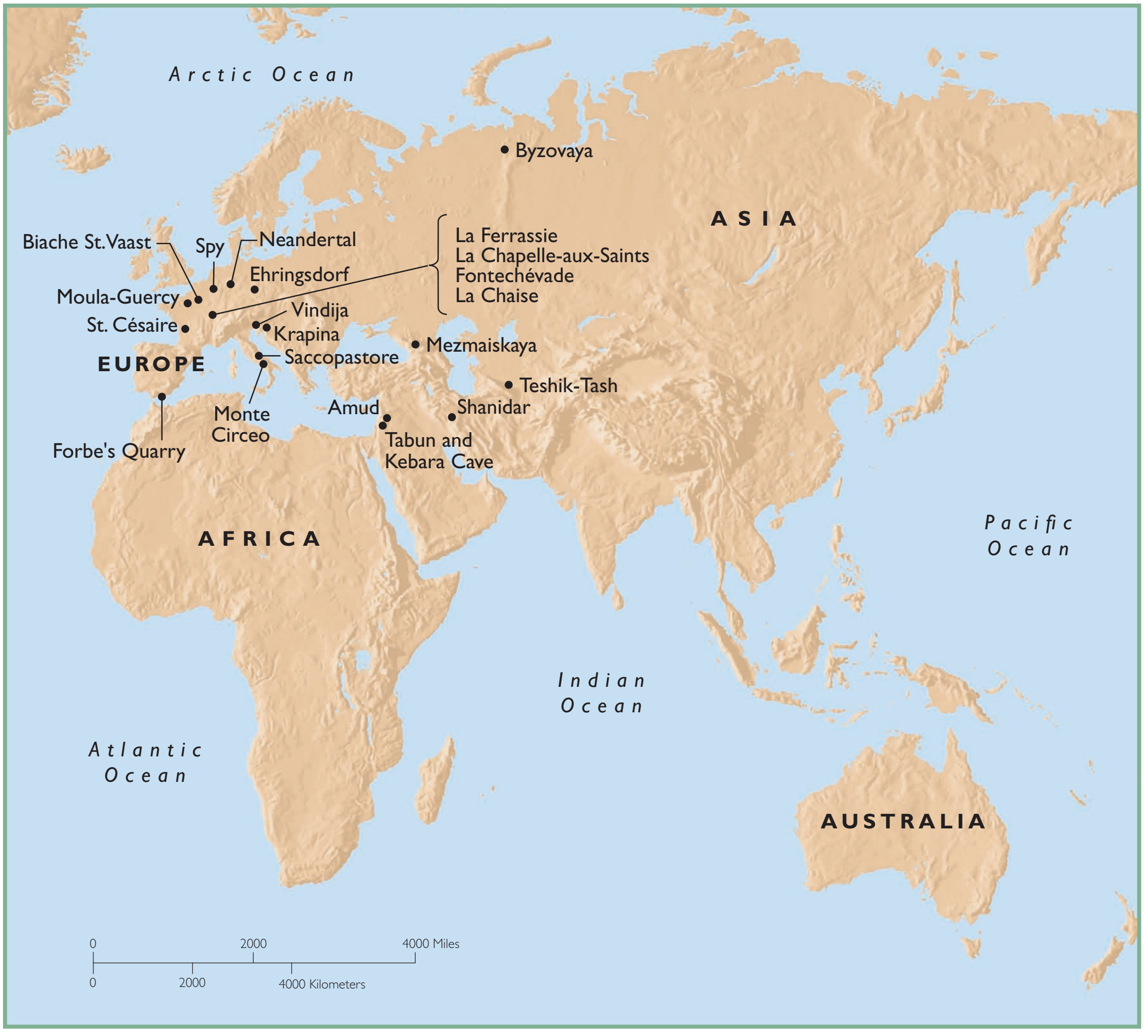

Arctic Ocean
Byzovaya
ASIA
Biache St.Vaast
Spy
Neandertal
Ehringsdorf
La Ferrassie
La Chapelle-aux-Saints
Fontechévade
La Chaise
Moula-Guercy
Vindija
St. Césaire
Krapina
Mezmaiskaya
EUROPE
Saccopastore
Teshik-Tash
Amud
Shanidar
Monte Circeo
Tabun and Kebara Cave
Forbe's Quarry
AFRICA
Pacific Ocean
Indian Ocean
Atlantic Ocean
AUSTRALIA
0
2000
4000 Miles
0
2000
4000 Kilometers

FIGURE 11.26
Map of major Neandertal sites.

(Figure 11.27). We now recognize the sophistication of the Neandertals' intellectual and cultural achievements. They were certainly similar to modern humans physically but still different in significant ways. So debate at present centers on whether the similarities place them within our species or whether the differences make them a separate species. Figures 11.28 and 11.29 compare the skulls and skeletons of a Neandertal and a modern *Homo sapiens*.

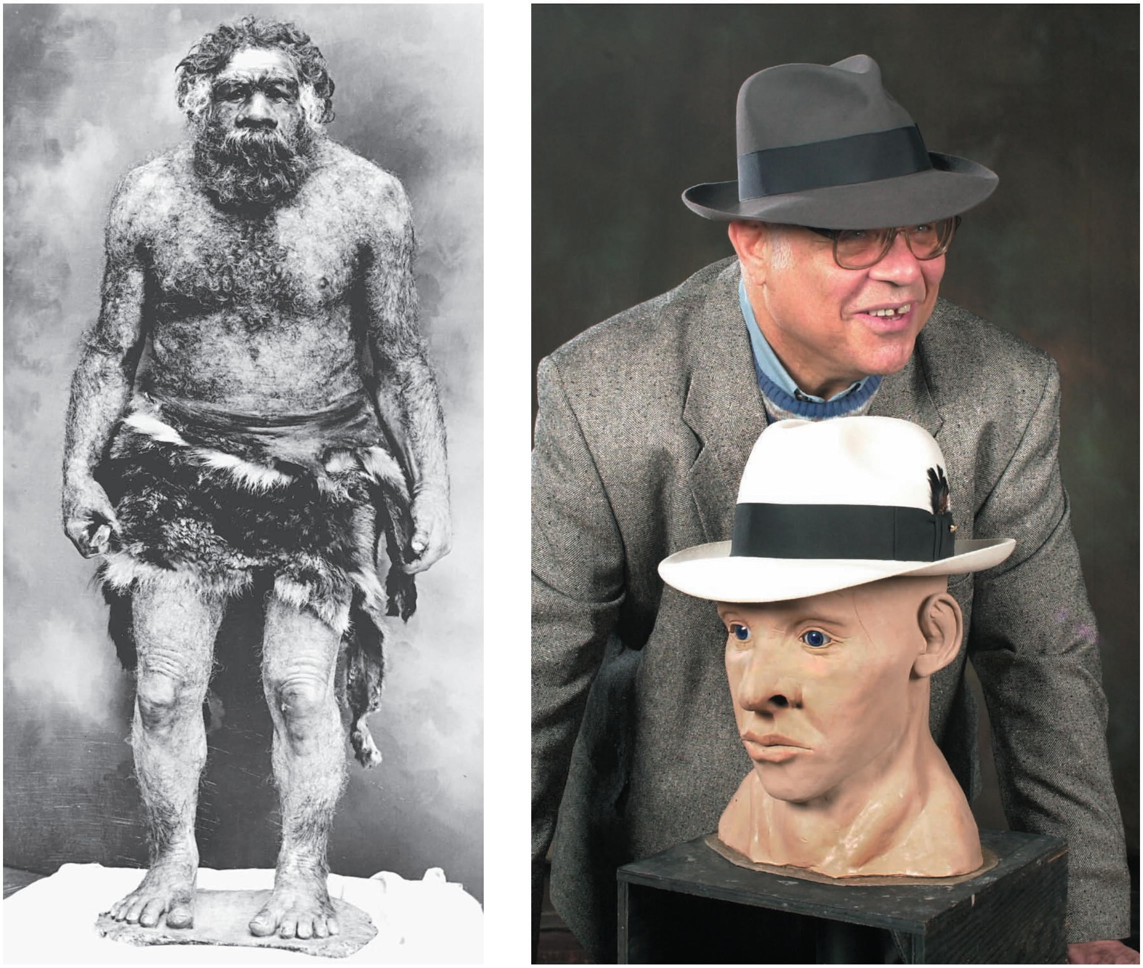


FIGURE 11.27
An old reconstruction from the Field Museum in Chicago (*left*) reinforces stereotypes of Neandertals as brutish, hairy, stooped-over distant cousins. In contrast, anthropologist Milford Wolpoff poses with a reconstructed Neandertal in modern dress to show that the differences between us and them were not that extreme.

Physical Features

The crania of the Neandertals are striking in appearance. Their cranial capacities ranged from about 1,200 ml to 1,740 ml, well within the modern range, but their foreheads were still sloped, the backs of their skulls broad, and the sides bulging. The brow ridges were still large, but smaller

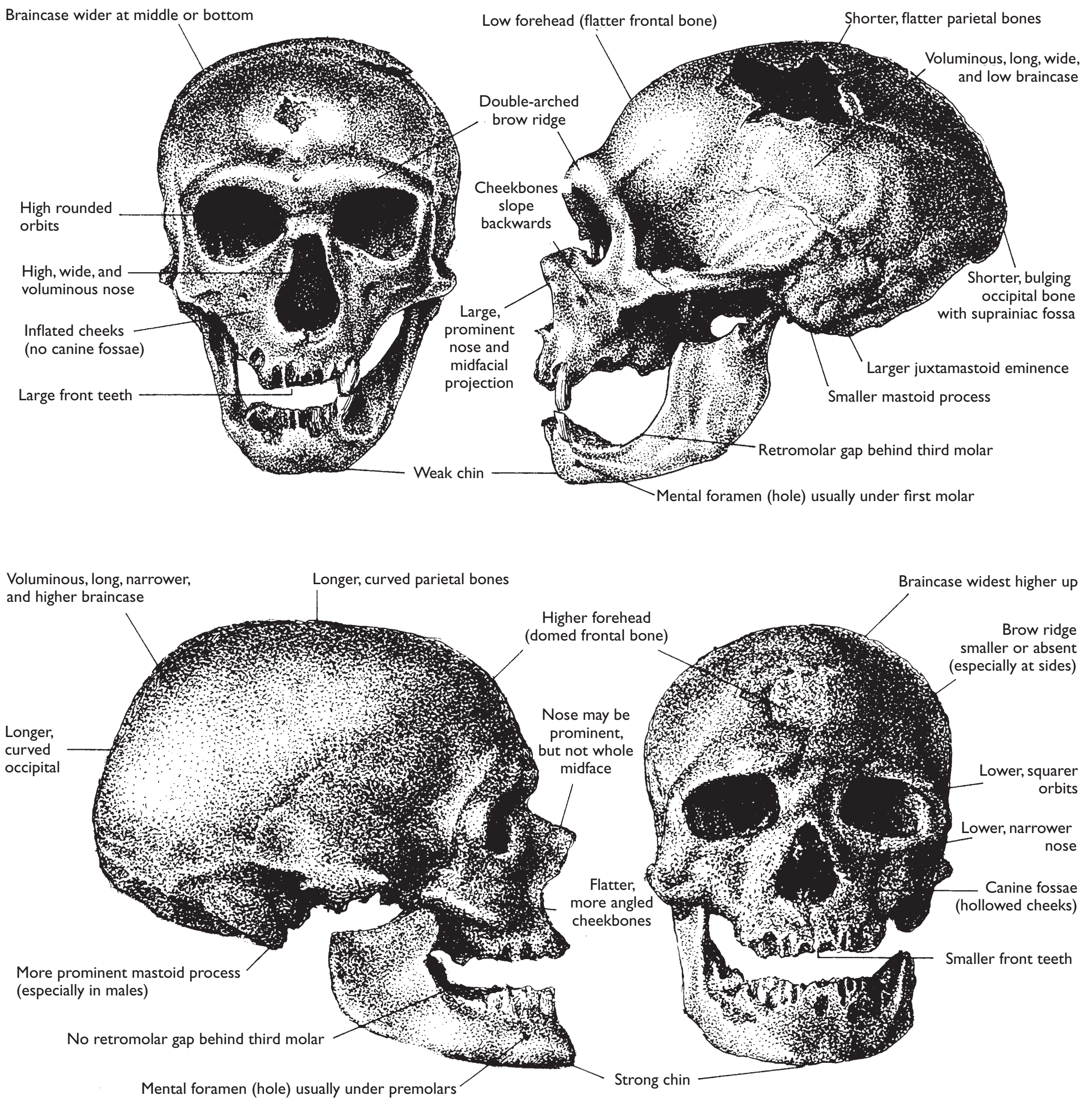
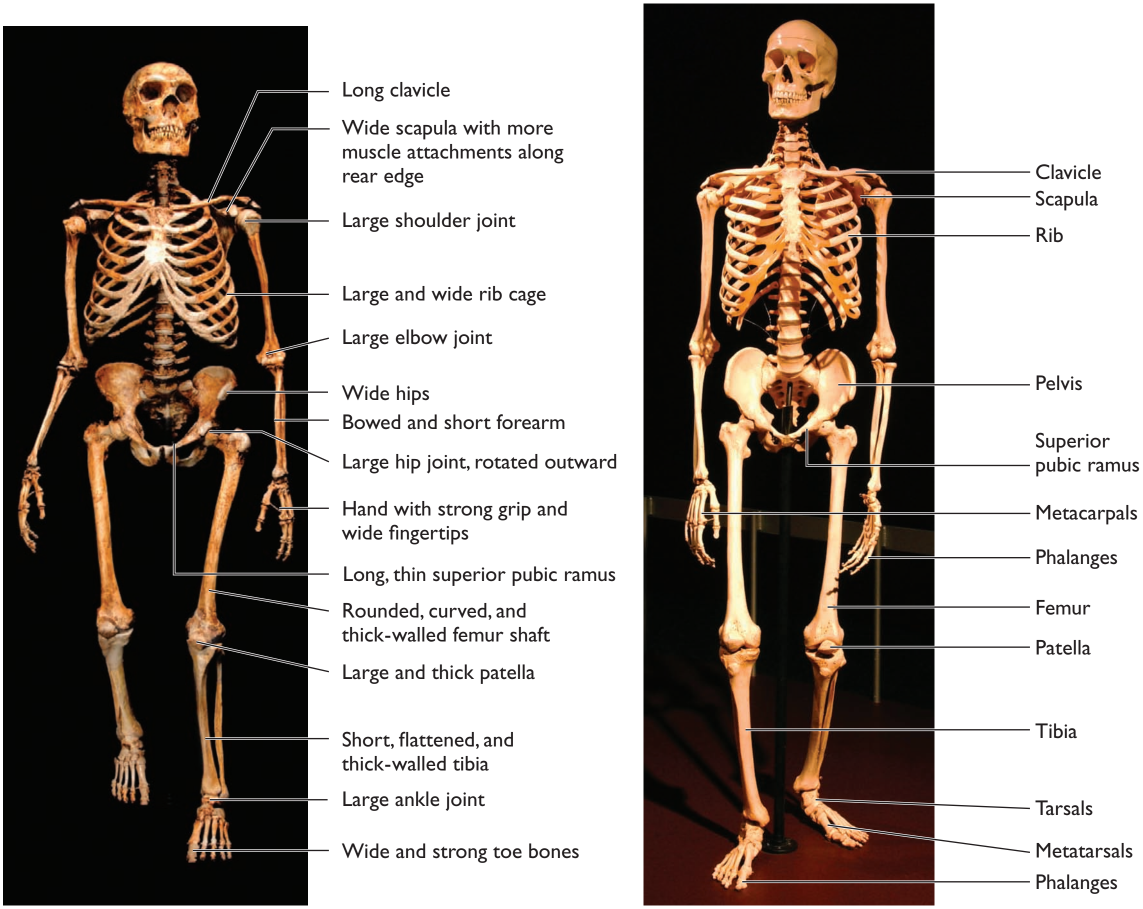

Braincase wider at middle or bottom
Low forehead (flatter frontal bone)
Shorter, flatter parietal bones
Voluminous, long, wide, and low braincase
Double-arched brow ridge
Cheekbones slope backwards
High rounded orbits
High, wide, and voluminous nose
Inflated cheeks (no canine fossae)
Large front teeth
Large, prominent nose and midfacial projection
Shorter, bulging occipital bone with suprainiac fossa
Larger juxtamastoid eminence
Smaller mastoid process
Retromolar gap behind third molar
Weak chin
Mental foramen (hole) usually under first molar
Voluminous, long, narrower, and higher braincase
Longer, curved parietal bones
Braincase widest higher up
Higher forehead (domed frontal bone)
Brow ridge smaller or absent (especially at sides)
Longer, curved occipital
Nose may be prominent, but not whole midface
Lower, squarer orbits
Lower, narrower nose
Flatter, more angled cheekbones
Canine fossae (hollowed cheeks)
Smaller front teeth
More prominent mastoid process (especially in males)
No retromolar gap behind third molar
Strong chin
Mental foramen (hole) usually under premolars

FIGURE 11.28
Cranial features of the La Chapelle-aux-Saints specimen of Neandertal (*above*) compared with modern *Homo sapiens*.

at the sides than in *H. erectus*, and they were filled with air spaces (called the *frontal sinuses*), unlike the solid ridges of *H. erectus*. The brow ridges of the Neandertals were also rounded over each eye, rather than forming a straight line, as in earlier archaics. The face was large and prognathous, with a broad nasal opening and wide-set eyes. The chin was receding.


Long clavicle
Wide scapula with more muscle attachments along rear edge
Large shoulder joint
Large and wide rib cage
Large elbow joint
Wide hips
Bowed and short forearm
Large hip joint, rotated outward
Hand with strong grip and wide fingertips
Long, thin superior pubic ramus
Rounded, curved, and thick-walled femur shaft
Large and thick patella
Short, flattened, and thick-walled tibia
Large ankle joint
Wide and strong toe bones
Clavicle
Scapula
Rib
Pelvis
Superior pubic ramus
Metacarpals
Phalanges
Femur
Patella
Tibia
Tarsals
Metatarsals
Phalanges

Neandertal

Modern *Homo sapiens*

FIGURE 11.29 Skeletal features of Neandertal compared with modern *Homo sapiens*.

From the neck down, there were striking features. The bones of the Neandertals, even the finger bones, were more robust and had heavier muscle markings than their modern counterparts. The Neandertals were stocky, muscular, powerful people. This is seen even in the bones of Neandertal children, so it is assumed to be a result of inheritance, not simply of a hard-working lifestyle.

Although very strong and stocky, the Neandertals were relatively short. Estimates put the average for males at 5 feet 6 inches and for females at 5 feet 3 inches. Their short stature was partially a result of relatively short lower legs. The lower arms were short as well. All these physical features hint at adaptations to a strenuous lifestyle and to cold climates. Shorter, heavier bodies with short limbs conserve heat better than narrow, long-limbed bodies (Holliday 1997; see also Chapter 12). As evidence, the limbs of the Neandertals from warmer Southwest Asia are relatively longer than the limbs of those living in ice-age Europe, who faced some of the extreme climates of the glacial advances.

Another possible adaptation to cold has been suggested by several investigators (Menon 1997). In eight Neandertal skulls, they found triangular bony projections in the nasal cavity unlike anything seen in modern humans or in any other human ancestors. These projections are thought to have provided increased surface area for the nasal mucous membranes, which would have helped warm and moisten the cold, dry air of Europe during the Pleistocene glaciations. It has also been suggested that the large sinus cavities served a similar function. Moreover, it is thought that the larynx of the Neandertals was higher in the throat than in modern humans (see Figure 11.18), which would have prevented them from gulping in cold, dry air through the mouth.

Well-established Neandertal fossils date from 225,000 to 28,000 ya, and, as Table 11.3 and Figure 11.26 indicate, are found in Western Europe, the Middle East, and possibly Russia (Balter 2011) and Uzbekistan. There are some tools of the kind associated with Neandertals (see the next section) from Gibraltar that are younger than 28,000 years, but there are no human remains yet at that date (Finlayson et al. 2006).

Culture

Tools Among the well-established accomplishments of the Neandertals is an elaboration on the Levallois stone toolmaking technique. Called the **Mousterian technique,** after the site of Le Moustier in France, it involved the careful retouching of flakes taken off cores. These flakes were sharpened and shaped by precise additional flaking, on one side or both, to make specialized tools (Figure 11.30). One authority has identified no less than sixty-three tool types (Bordes 1972).

Several specific uses of Mousterian tools have been inferred from microscopic wear-pattern analysis on specimens from the Kebara Cave site in Israel. There are wear patterns that indicate animal butchering, woodworking, bone and antler carving, and working of animal hides (Shea 1989). There are also wear patterns like those produced by the friction of a wooden shaft against a stone spear point. The Neandertals may have been the first to **haft** a stone point.

Mousterian technique A toolmaking tradition associated with the European Neandertals.

haft To attach a wooden handle or shaft to a stone or bone point.

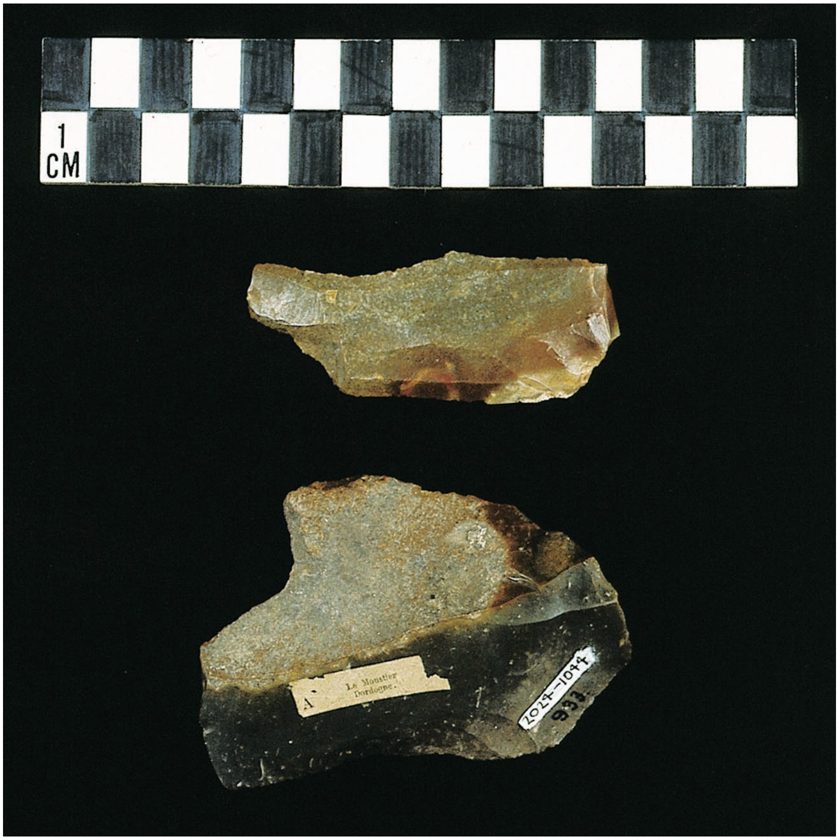


FIGURE 11.30
Unifacially retouched Mousterian flakes from the original site, Le Moustier, France.

Although there is still debate about whether the Neandertals were big-game hunters or mostly scavengers, there is no doubt that they were dependent on the animals that abounded during the Pleistocene—animals such as reindeer, deer, ibex (wild goat), aurochs (wild ox), horse, woolly rhinoceros, bison, bear, and elk. Bones of these creatures have been found in association with Neandertal remains.

Burials While we now have earlier evidence of intentional human burials, the first and most famous evidence comes from the Neandertals. Although many of these "burials" have now been attributed to natural causes, at least thirty-six Neandertal sites show evidence of intentional interment of the dead, and in some graves there were remains of offerings—stone tools, animal bones, and, possibly, flowers (Figure 11.31).

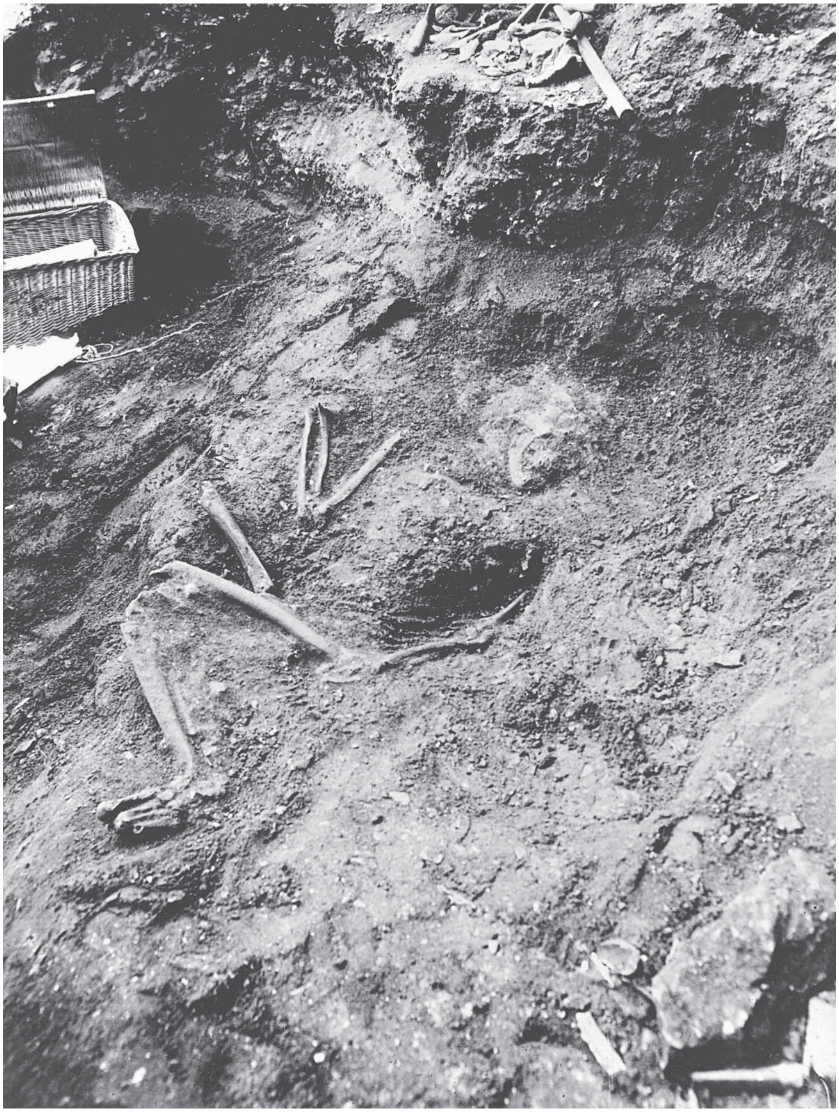


FIGURE 11.31
Neandertal burial from La Ferrassie, France. This body was interred in the flexed position, with the knees drawn up to the chest, perhaps to mimic sleep. (The basket belongs to the excavators.)

Did the burials represent belief in an afterlife or reverence for the physical remains of the deceased, or were the people simply disposing of a corpse, as seems to have been the case much earlier at Sima de los Huesos? Were animal bones present in the graves as offerings, or did scavengers and predators drag them there, along with Neandertal bones, where they were

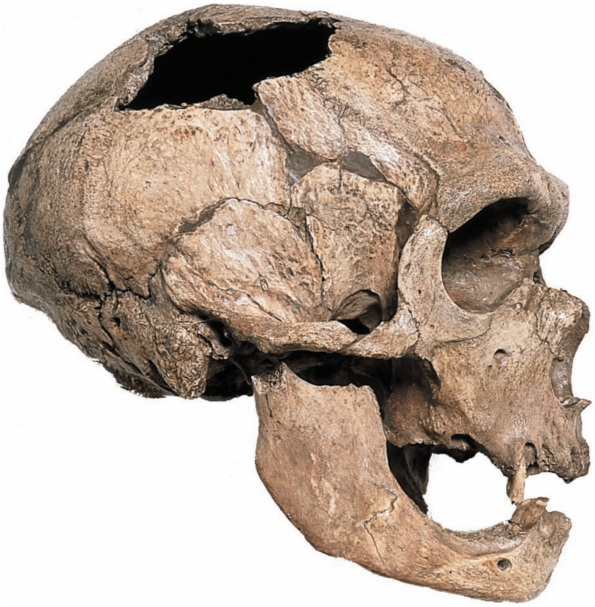


FIGURE 11.32
The famous "Old Man" of La Chapelle-aux-Saints, France. (See front view and labels in Figure 11.28.)

subsequently buried by natural processes? Was the pollen found in a grave in Iraq from flowers placed in the grave, or was it brought in by burrowing rodents, carried in by water, or blown in by wind at the time of burial? The jury is still out on this issue. But we know the Neandertals did sometimes bury their dead, for whatever reason.

Care of the Infirm and Elderly. The famous "Old Man" of La Chapelle-aux-Saints in France (Figure 11.32) had lost many of his teeth, and had arthritis. That he survived for a time with these infirmities, according to the common interpretation, indicates that he was cared for by his group. But he wasn't that old. He died when he was less than 40, probably rather quickly, as did the vast majority of Neandertals. Care of the elderly was probably not something they had to contend with very often.

But there is a skeleton of a man from Shanidar, Iraq, that shows signs of injuries that may have resulted in blindness and the loss of one arm. He lived with this condition for some time and, therefore, was obviously cared for by his comrades.

But things may not have been completely peaceful among Neandertal populations. There is evidence of cannibalism from the Neandertal sites of Moula-Guercy in France (Defleur et al. 1999) and Krapina and Vindija in Croatia (White 2001). Fragmentary bones from at least six individuals show stone-tool cut marks in the same anatomical locations as those found on bones of wild goats and deer at the site. Some of the human long bones also show signs of having been smashed, in the way that would have allowed access to the rich bone marrow. Whether the inferred cannibalism was ritual (ingesting part of a group member at a funeral ceremony) or gustatory (eating the flesh as food) cannot be determined.

Language Finally, we have the question of the linguistic abilities of the Neandertals. Some investigators have reconstructed the vocal tract of Neandertals based on the structure of the underside of the cranium. They have concluded that because of the higher larynx noted before, Neandertals were not capable of making all the vowel sounds of modern humans. However, a recently found hyoid bone—a horseshoe-shaped bone in the throat—from the Neandertal site of Kebara in Israel appears fully modern. This would mean that the vocal tract of the Neandertals *was* like ours and that they *could* make all the sounds of which we are capable. The point, of course, is—as we said for *Homo erectus*—that the Neandertals had sufficiently complex things to talk *about*, and just how they did so is less important than the fact that they must have talked.

Archaic members of genus *Homo* were successful in adapting to different environments and, in the case of the Neandertals, harsh and demanding climates. They were clearly intelligent. We will no doubt find more fossils of archaics in new areas in the future. But the archaics have combinations of traits not found in humans alive today. To begin the story of so-called anatomically modern *Homo sapiens*, we once again return to Africa.

MODERN HUMANS

Beginning perhaps as early as 300,000 ya, fossils with what are considered to be near-modern or modern combinations of features appear, earliest in Africa and later in Southwest Asia, Europe, and East Asia. Later still, modern humans migrated to Australia, the islands of the Pacific, and North and South America. Under the six-species model, fossil forms with modern features are the only ones placed in *Homo sapiens*. There is no general agreement among proponents of this model about the exact species affiliation of some transitional forms—fossils with a mix of archaic and

TABLE 11.4
Some Important Fossils of Early *Homo sapiens* (listed chronologically)

Country	*Location*	*Age (years)*
Kenya	Ileret	270,000–300,000 (trans.)*
South Africa	Florisbad	100,000–200,000 (trans.)
China	Zhirendong	100,000 (trans.?)
Ethiopia	Omo	195,000 (trans.)
Tanzania	Ngaloba	120,000 (trans.)
Morocco	Jebel Irhoud	100,000 (trans.)
Ethiopia	Herto	154,000–160,000
South Africa	Klasies River Mouth	84,000–120,000
	Langebaan Lagoon (footprints)	117,000
	Border Cave	62,000–115,000
	Hofmeyr	36,000
Israel	Qafzeh	92,000–120,000
	Skhul	81,000–101,000
Germany	Stetten	36,000
France	Cro-Magnon	<30,000
	Abri Pataud	>27,000
China	Zhoukoudian	10,000–18,000
Australia	Lake Mungo	40,000
United States	Midland, Texas	11,600

*The abbreviation *trans.* indicates those fossils that are considered transitional between archaic and modern *Homo*.

modern traits. Table 11.4 and Figure 11.33 give the basic information and locations of some of the more important fossils of early *H. sapiens*, as well as transitional forms.

Anatomy

We call these fossils "anatomically modern" because they lack some features characteristic of earlier hominids and possess features common in humans today. According to a widely accepted definition, the anatomically modern human does not exhibit a prognathous profile; the face is flat. There are no heavy brow ridges. The skull is globular rather than elongated, and the forehead is more nearly vertical. The face is smaller and narrower, and there

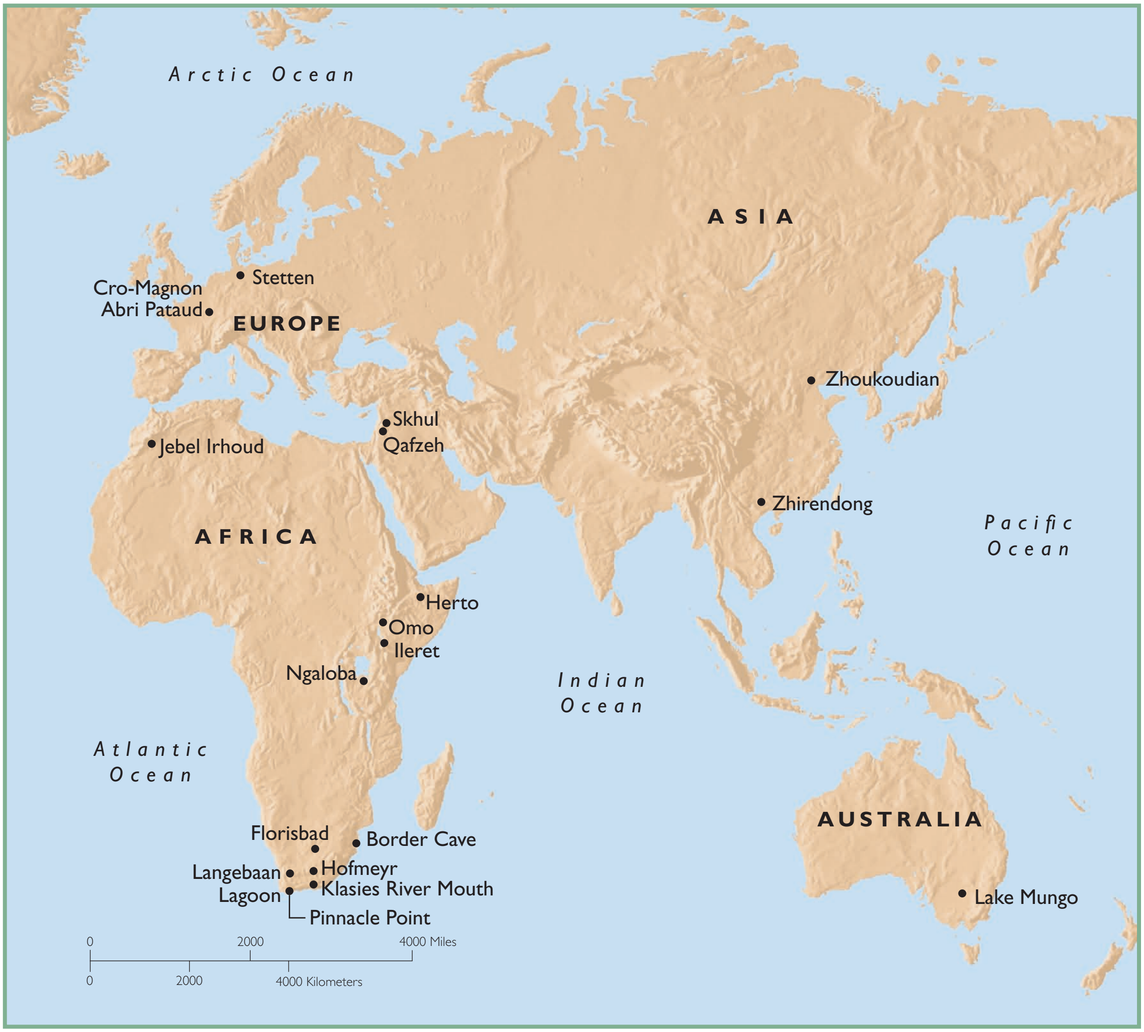

Arctic Ocean
ASIA
EUROPE
Stetten
Cro-Magnon
Abri Pataud
Zhoukoudian
Skhul
Qafzeh
Jebel Irhoud
Zhirendong
Pacific Ocean
AFRICA
Herto
Omo
Ileret
Ngaloba
Indian Ocean
Atlantic Ocean
AUSTRALIA
Florisbad
Border Cave
Langebaan Lagoon
Hofmeyr
Klasies River Mouth
Pinnacle Point
Lake Mungo
0
2000
4000 Miles
0
2000
4000 Kilometers

FIGURE 11.33
Map of major early *Homo sapiens* sites in Africa, Asia, Australia, and Europe noted in table or text.

is a protruding chin. The postcranial skeleton is less robust. Refer back to Figures 11.28 and 11.29, and then look in the mirror.

Dates

Note in Table 11.4 that the earliest fossils are all from eastern and southern Africa and that they are considered, at least by some authorities, as

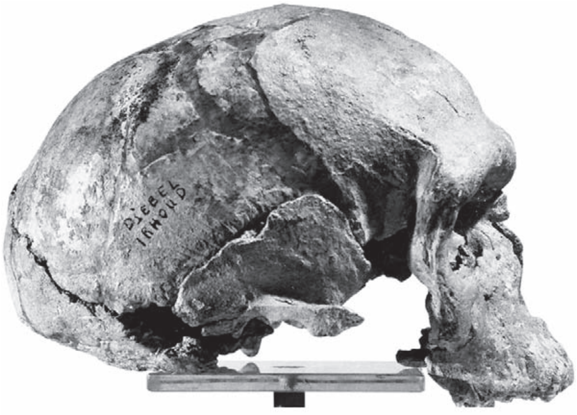


FIGURE 11.34
Cranium from Jebel Irhoud, Morocco. This skull, dated at about 100,000 ya, is considered by some to be transitional between archaic and modern *Homo*. The braincase is low, the face is relatively large, and it has distinct brow ridges. Otherwise, its features are modern.

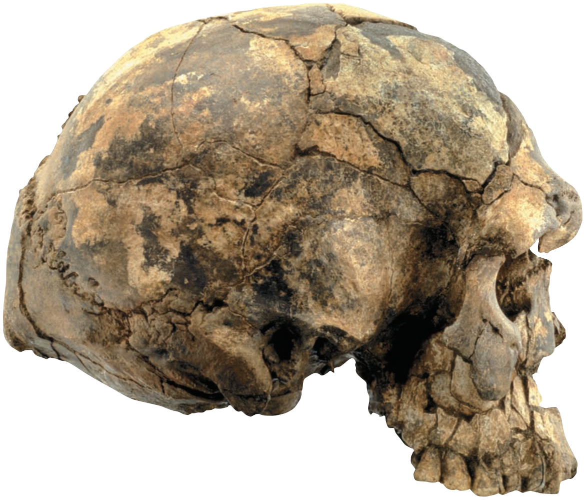


FIGURE 11.35
The most complete early *Homo sapiens* skull from Herto, Ethiopia, dated at 160,000 ya. The wide upper face, rounded forehead, divided brow ridge, flat midface, and large cranial capacity are all modern traits.

transitional between archaic and modern *Homo*. There is also a transitional form from Morocco (Figure 11.34), and a possible, although controversial one from China. The implication is that modern humans—whether a new species or just the modern form of an existing species—arose in Africa. The earliest transitional forms are from Kenya, dated by several methods to 300,000 ya (Braüer et al. 1997).

By around 160,000 ya, we begin to find fossils that represent humans of fully modern appearance relative to their geographic area. The earliest of these are recent finds from Ethiopia (Figure 11.35) (Clark et al. 2003; White et al. 2003) that are "oldest definite record of what we currently

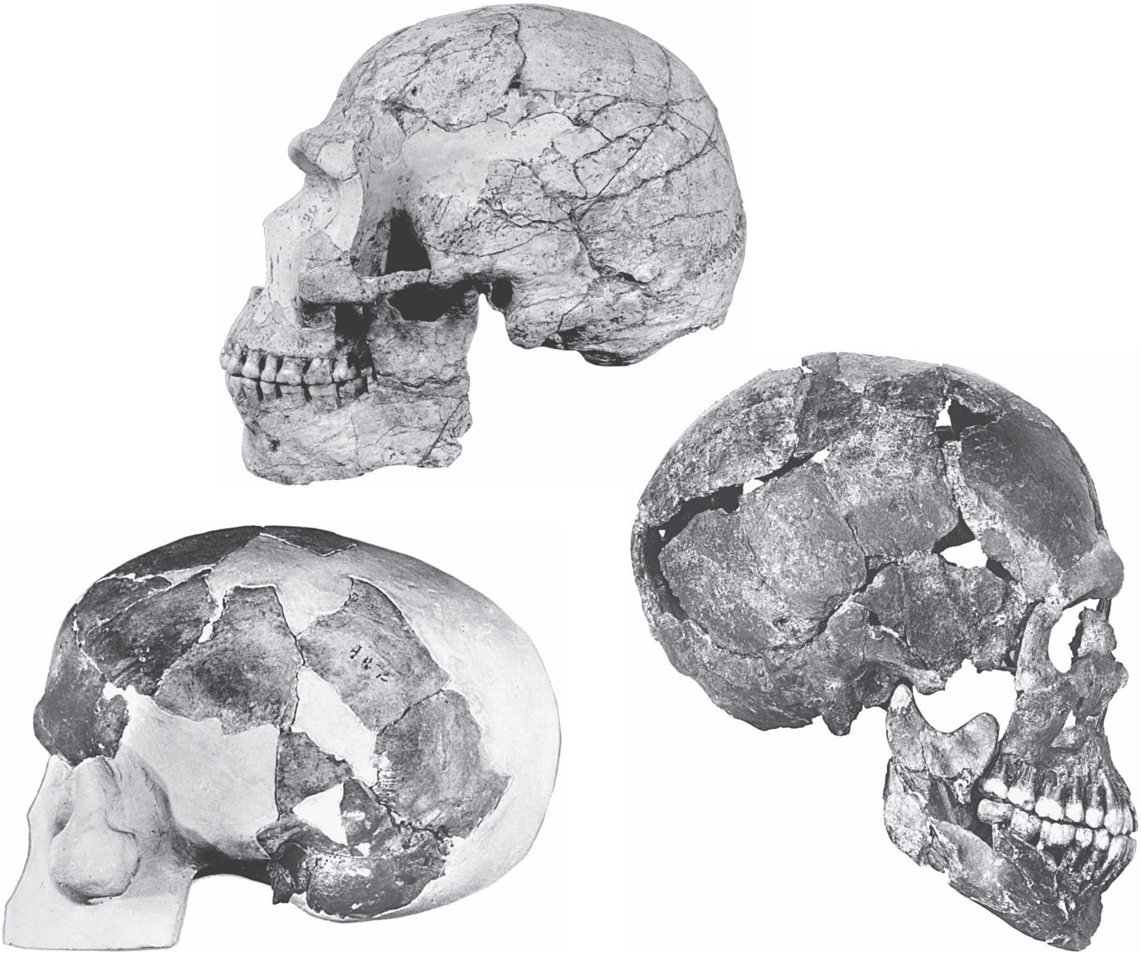


FIGURE 11.36
Examples of early modern *Homo sapiens* from (*counterclockwise from top*) Skhul, Israel; Border Cave, South Africa; and Qafzeh, Israel. Note the higher foreheads, protruding chins, and flatter faces compared with archaic *Homo*. Despite the rather prominent brow ridges in the Skhul specimen, it is still considered fully modern due to its other features.

think of as modern *Homo sapiens*" (Stringer 2003). These remains are associated with a mix of primitive and more sophisticated stone tools.

Slightly more recent fossils are from South Africa and Israel (Figure 11.36). At the South African site of Langebaan Lagoon, a small human, possibly a female, left her footprints in rock claimed to be dated 117,000 ya—a moment frozen in time reminiscent of the Laetoli footprints from Tanzania (see Chapter 10). As we move farther away from Africa and Southwest Asia, the dates for the early appearance of modern *H. sapiens* get more recent, a further indication that Africa is the birthplace of modern humans.

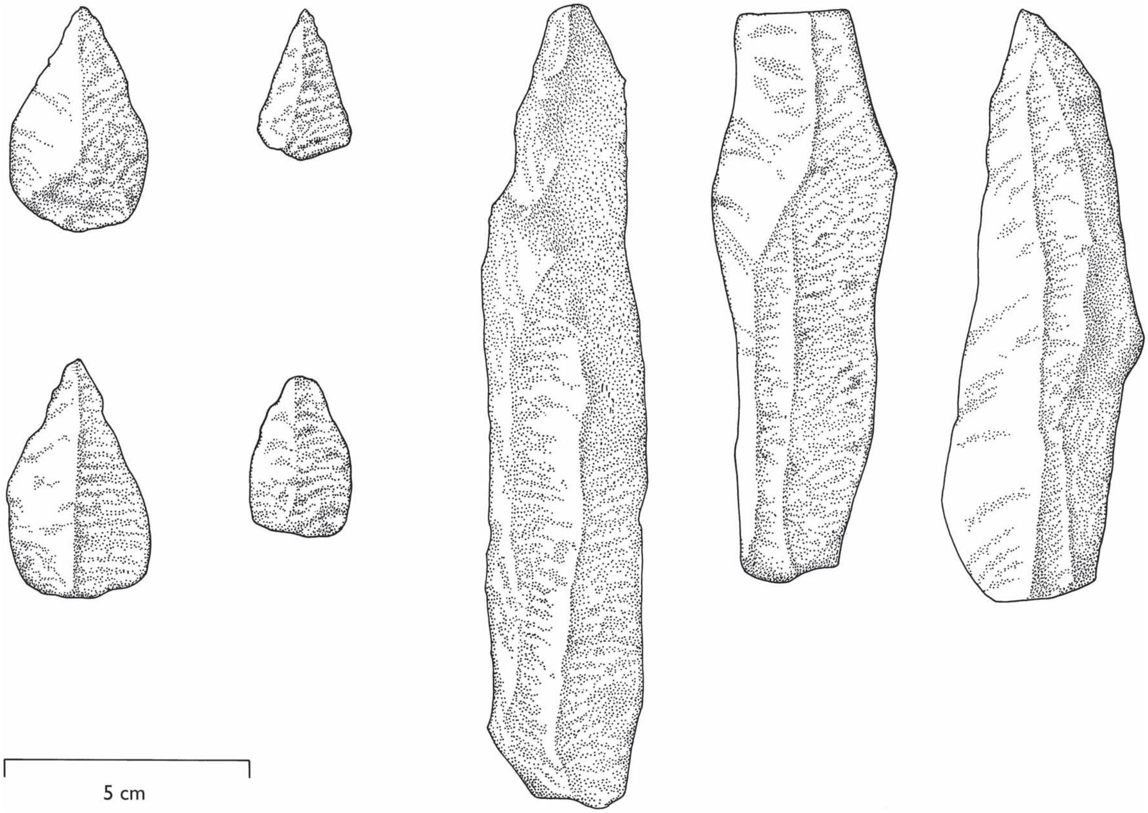


FIGURE 11.37
Blade tools from Klasies River Mouth, South Africa.

Culture

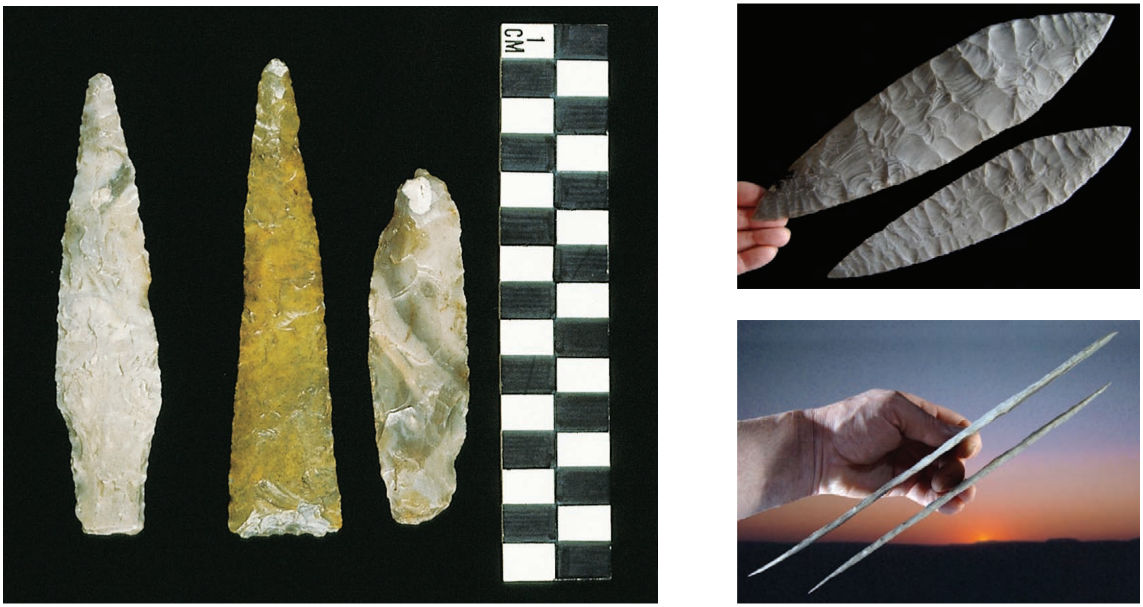
With modern anatomy came further advances in technology and expressions of modern behavior patterns. From the Pinnacle Point site, on the coast of South Africa and dated at 165,000 ya, we find evidence of shellfish used for food, of iron oxide used possibly as a pigment (with some of the pieces incised as decoration or maybe even a "notational system"), and of miniature stone tools called "bladelets" (Marean et al. 2007). A little later, from 120,000 ya at Klasies River Mouth, also on the South African coast, come long, bifacially worked spear points made from stone blades. These were flaked from cores by the *punch technique* (Figure 11.37). Here a pointed punch, usually made from an antler, is placed on the core and then struck with a stone hammer. This method directs the force of the blow more precisely so that longer, narrower, thinner flakes of predictable shape may be taken off. The same technique shows up later in Europe.

The Klasies River site also provides evidence that the people there may have hunted adults of such large animals as cape buffalo and eland (a large antelope); both of these animals can weigh up to a ton. The site contains a spear point lodged in a buffalo vertebra, good evidence of at least limited big-game hunting. That behavior, it seems, can be associated with the appearance of anatomically modern humans.

Although the Neandertal burials are perhaps the most famous examples of early human symbolic behavior, it is at two of the early *Homo sapiens* sites that we find the earliest examples. In Israel there are graves, dated at between 120,000 and 80,000 ya, with bodies and grave goods carefully laid out. In one grave, a child was buried with a deer antler. Another grave at the same site contained the body of a young woman with that of an infant, possibly hers, at her feet. At another site, a skeleton was found holding the jawbone of a wild boar.

By the time the Neandertals apparently disappeared, about 30,000 ya, modern *H. sapiens* had spread all over the Old World, even as far as Australia, and we enter a cultural period called the Upper Paleolithic, known first through finds in Europe. This period is marked by several important cultural innovations. Blades struck off cores become so precisely and beautifully made as to be virtual works of art—in fact, some blades are so thin and delicate we think they may have been just that (Figure 11.38).

FIGURE 11.38
Some typical Upper Paleolithic tools and examples of blades so finely made and thin they were probably used ritually.



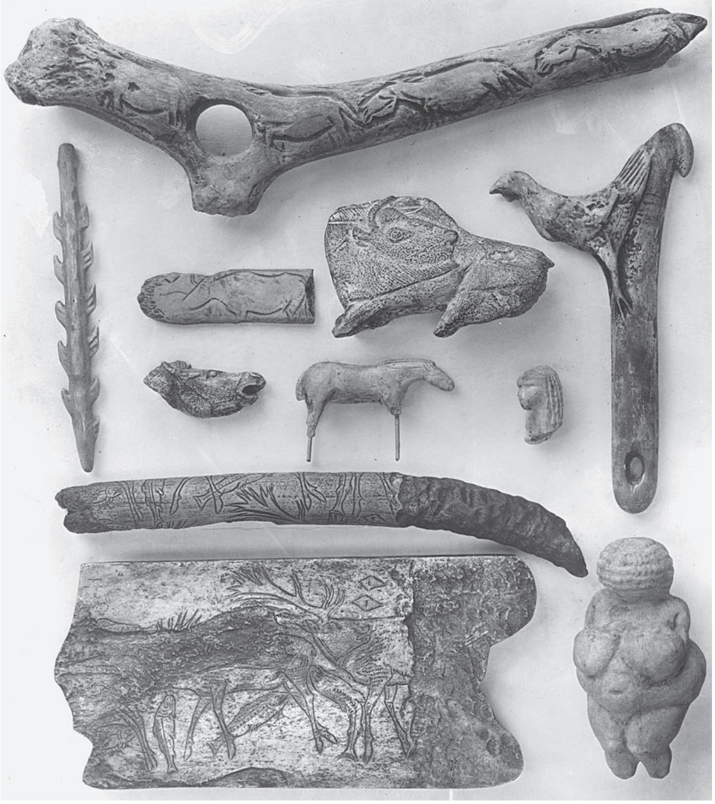


FIGURE 11.39
Upper Paleolithic artifacts. Among the artifacts shown here are a shaft straightener with carved animals (*top*), a harpoon carved from antler (*upper left*), and an example of the famous Venus figurines (*lower right*) that may have served as fertility symbols.

Tools in the Upper Paleolithic were also made from bone, antler, and ivory. Some are practical, such as harpoons, spear points, and shaft straighteners. Some have symbolic significance. Even some of the utilitarian items are decorated (Figure 11.39). Indeed, art is seen in the Upper Paleolithic in some of its most striking and beautiful forms. Over a hundred cave sites, mostly in France and Spain, have yielded paintings as aesthetically pleasing as anything produced today (Figure 11.40). There are also carvings in stone, bone, antler, and ivory, among the most famous of which are the so-called Venus figurines, often thought to be fertility symbols (see Figure 11.39, lower right). Some Venus figurines even depict clothing styles such as woven caps (Wong 2000a). An ivory "lion man" figurine from Germany, dated at 30,000 ya, may be the oldest figurative art in the world. There is also an engraved antler from France dated at about 32,000 ya that may have been a calendar based on phases of the moon.

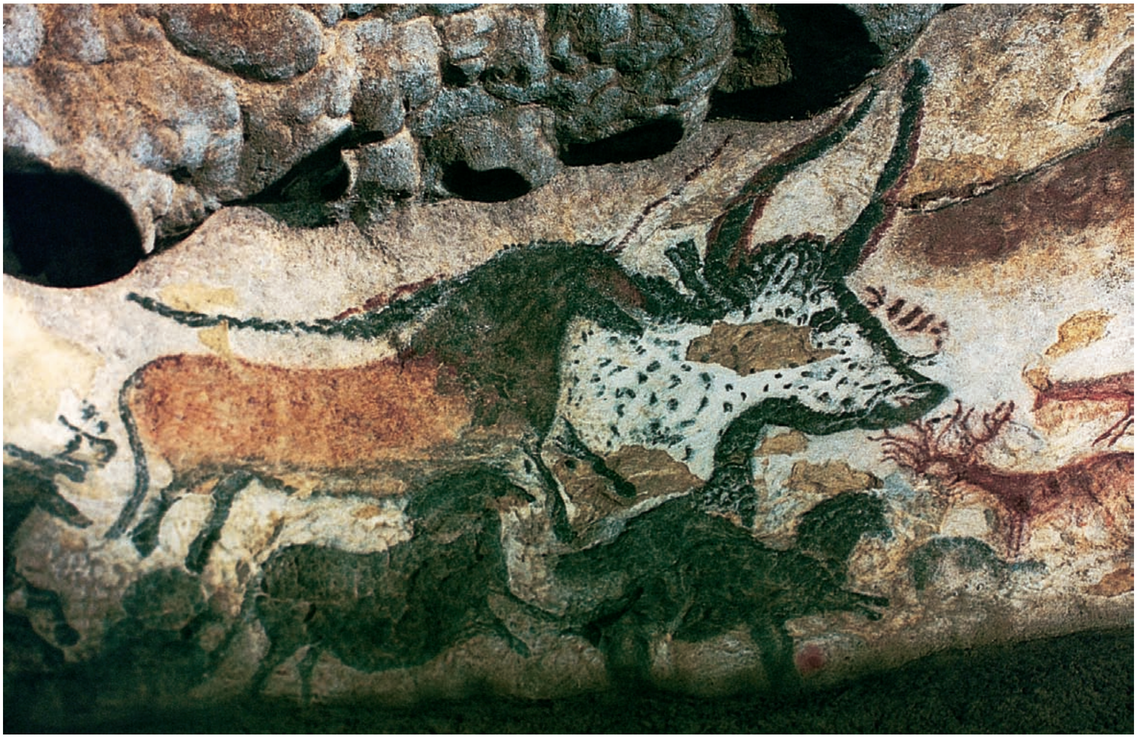


FIGURE 11.40
One of many beautiful paintings from the cave of Lascaux in southern France, this mural depicts an aurochs (an ancient ox) and several horses. There is an antlered animal, probably a deer, in the lower right. Notice that the left front leg of the red horse is separated from the body, adding a three-dimensional appearance. This photograph is really from Lascaux II, a replica near the actual cave, created because of damage to the original from bacteria and carbon dioxide given off by too many visitors. The walls of the replica cave are reproduced to within 5 mm of the contours of the original cave, and many of the pigments in the paintings are the same as those used by the original artists perhaps 17,000 ya.

There is some evidence of even older art from northern Australia. An iron-oxide "crayon" has been dated at almost 60,000 ya and painted ocher figures and carved holes at a rock shelter site may date to between 176,000 and 116,000 ya. Dating of these sites remains debatable (Gibbons 1997a).

As the Upper Paleolithic continued, big-game hunting became a way of life, especially for people living in glacial climates with limited plant resources. People no longer relied on caves or rock shelters for places of habitation but began manufacturing shelters. At an 18,000-year-old site in south-central Russia, scientists found the remains of a hut built on a

Contemporary Reflections

Who Are the "Hobbits" from Indonesia?

In October 2004 an astonishing find was announced (Brown et al. 2004). A partial human skeleton, dated to 18,000 ya, was discovered on the Indonesian island of Flores. What makes this find remarkable is that the skeleton is of an adult female who stood a mere 106 cm tall (about 3 feet 5 inches) and had an estimated brain size of 380 ml, about the stature and cranial capacity of *Australopithecus afarensis*. And yet the physical features seem fairly clearly to assign the specimen to genus *Homo*, with particular similarities to *Homo erectus*. The discoverers gave the specimen the status of a new species, *Homo floresiensis* (Figure 11.41).

Since this initial discovery (Morwood et al. 2005), more specimens have been announced—including arm, wrist, and foot bones of the original skeleton, a mandible from a second individual, and assorted other bones—from an estimated nine individuals in all. Dates range from 74,000 (and possibly 95,000) to 12,000 ya.

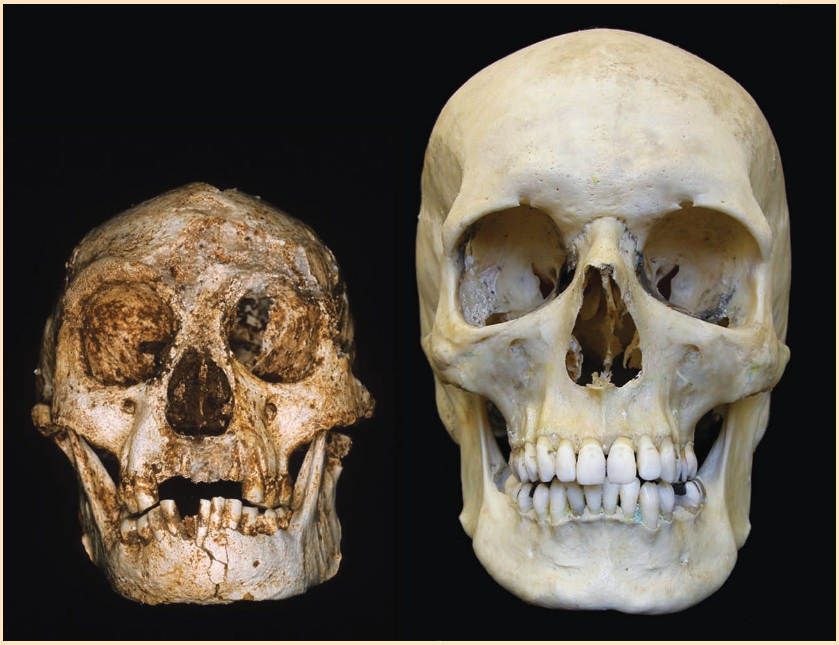


FIGURE 11.41
The skull of *Homo floresiensis* (*left*) compared to a modern human skull.

Even for those who propose multiple species of our genus over the last 2 million years, this is an amazing find, because as far as we know there have been no humans other than us—fully modern *Homo sapiens*—on earth for at least 27,000 years. And for those of us who feel that only one species of *Homo* has existed, the implications of this find and its interpretation are obvious.

What are we to make of these specimens, referred to in the popular press as Hobbits (a reference to the small characters in J. R. R. Tolkien's *Lord of the Rings*)? Given their body and brain size, could they be australopithecines, indicating that there were populations of this genus outside of Africa? Probably not. Although some authorities say the lack of a chin, features of the pelvis, and body proportions are australopithecine in nature (Balter 2004; Lieberman 2005), they have phenotypic characteristics that place them clearly in genus *Homo*. Moreover, the fossils were found in association with stone tools and evidence of hunting and possibly fire and cooking. None of these cultural features are associated with *Australopithecus*. And the game hunted was not small; it included pygmy elephants and Komodo dragons (the world's largest existing lizard). Certainly a high level of cooperation and communication would have been necessary to accomplish such hunting. Moreover, no fossils of australopithecines have been found outside of Africa.

Authorities are divided over the interpretation of these fossils, or, more accurately, over the original fossil, known as LB1, since it provides the vast majority of the data. Some contend it was an individual with a pathology, perhaps microcephaly, a genetic form of dwarfism (Eckhardt 2008). Other experts support the claim that LB1 represents a normal human of diminutive size but of a different species (Falk et al. 2008). The recently reported wrist bones are said to be "primitive" and thus indicative of a new species by some (Tocheri et al. 2007), while others disagree (Eckhardt 2008). Still others have concluded that because the feet are relatively long and not arched, as in modern humans, the Flores population represents a new species (Jungers et al. 2008). The discussions over this issue at professional meetings are at least lively and can get quite heated. (For a summary of the arguments at a recent meeting, see Culotta 2008.)

So, there was either one, or several, individuals on Flores during the time range indicated that suffered from some anomaly, or there was a whole population of diminutive humans. If the latter, there are two questions: First, were they a different species? We can't, of course, experiment to see if they could interbreed with other human populations, so that will always remain an open question. Second, where did they come from? Did they descend from *Homo erectus* and respond to a phenomenon of dwarfing common to island species with restricted room and resources? Or did a hominid predating *H. erectus* get to Flores and evolve a more complex brain with no increase in size (Aiello 2010)? Virtual images of the brain of LB1 indicate that it is not a miniaturized modern brain but more resembles *Paranthropus* in size and *H. erectus* in shape (Falk et al. 2005).

The debate continues and, of course, requires more data—specifically, more fossils. But one thing is certain: genus *Homo* is a lot more variable than we once imagined. And the story continues to unfold: on the island of Palau, Micronesia, researchers have found fossils of a possible small-bodied population with brains within the modern human range (Berger et al. 2008). Stay tuned.

wood frame supported by woolly mammoth bones and reindeer antlers and covered with animal hides.

Around 30,000 ya, and probably earlier, humans moved into North America, coming across a land bridge between Siberia and Alaska that was exposed when the sea level dropped during glacial periods. They soon moved throughout the continent and into South America. Modern *Homo sapiens* had populated every landmass on the planet except Antarctica.

MORE NEANDERTALS AND YET ANOTHER HUMAN GROUP?

In 2010 (Reich et al. 2010; Callaway 2011; Gibbons 2011c; Kolbert 2011), a new find was announced from Denisova Cave in Siberia, close to the borders of Kazakhstan, China, and Mongolia. Inhabited from 30,000 to 500,000 years ago, the cave yielded evidence assessed genetically and archaeologically as belonging to three different groups—Neandertal, modern human, and a new group dubbed the Denisovans. The actual physical evidence is minimal: a toe bone for the Neandertal, two molars and a bit of finger bone for the Denisovans, and some stone and bone artifacts for the modern human.The DNA of the bones of the Denisovans was considered distinct enough to warrant creating a whole new human group.

Some of the primary researchers have created a broad scenario with the Denisovans being a heretofore unknown group that lived all over eastern Asia, interbred a bit with Neandertals and modern humans, and even contributed about 5 percent to the gene pool of modern Melanesians and Native Australians.

As of this writing, there is debate about this interpretation and, clearly, much more evidence is needed before such a specific scenario, or any specific scenario, can be supported.

THE DEBATE OVER MODERN HUMAN ORIGINS

In the beginning of this chapter I mentioned that there are two opposing views on the origin of our species, *Homo sapiens*, and, thus, on the evolutionary relationships among all the groups of genus *Homo* we've been discussing. A complete examination of the arguments and analysis of the evidence can get extremely technical, but we can take a look at the issue here sufficiently for you to understand those basic arguments and evidence.

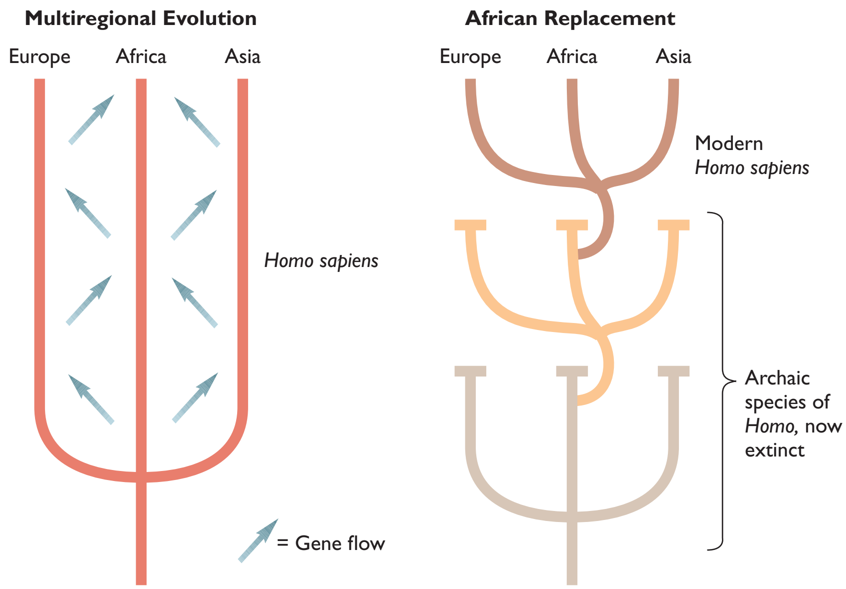

Multiregional Evolution
Europe
Africa
Asia
Homo sapiens
= Gene flow
African Replacement
Europe
Africa
Asia
Modern *Homo sapiens*
Archaic species of *Homo*, now extinct

FIGURE 11.42 Generalized models for the origin of *Homo sapiens*.

At this point the matter is unresolved, and may remain so, and I'll indicate why when we get to the end.

The Models

There are variations of each of these, but each can be easily summarized and diagrammed (Figure 11.42).

The Multiregional Evolution Model (MRE) This model says that *Homo sapiens* arose in Africa about 2 mya and spread from there across the Old World and subsequently to the Pacific and the Americas. During that time, there was sufficient mobility and gene flow to maintain us as a single species. As members of this species spread they evolved genetic and phenotypic regional differences in response to the wide variety of environmental circumstances they encountered, and to the complex population movements, isolations, mergings, and splits that must have taken place. (Review Figure 4.4.)But no population was isolated long enough or to a great enough degree for speciation to occur. (Refer to Chapter 5 to review the requirements for speciation.) As new and advantageous adaptive features arose, they were dispersed across the species through gene flow. Ideas and technologies spread and were exchanged as well (Wolpoff et al. 2001).

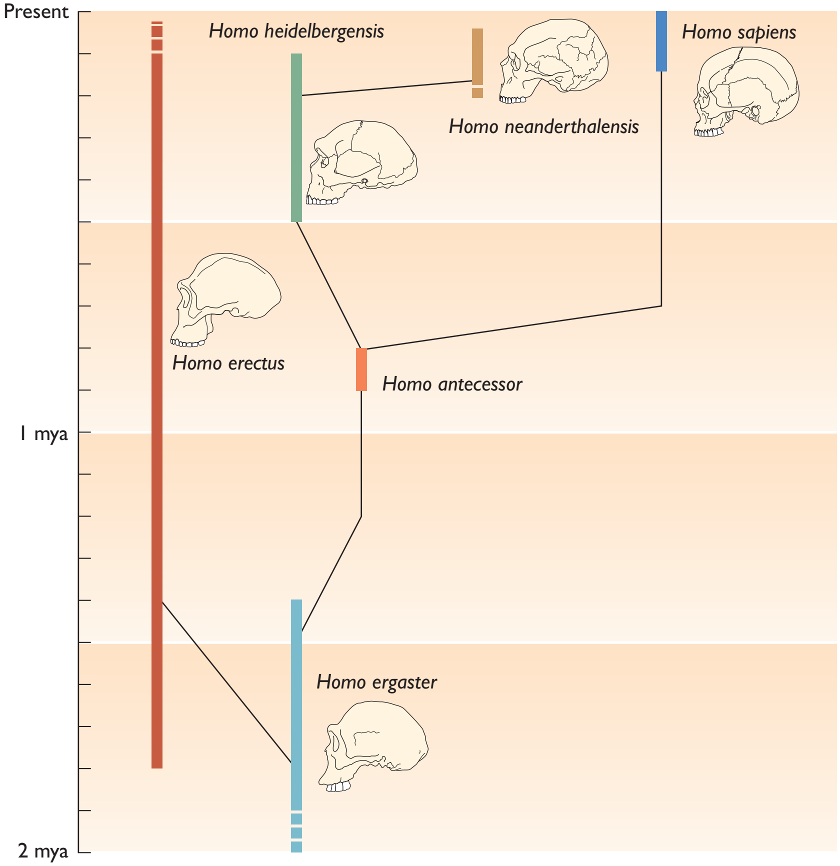

Present
1 mya
2 mya
Homo heidelbergensis
Homo neanderthalensis
Homo sapiens
Homo erectus
Homo antecessor
Homo ergaster

FIGURE 11.43 One possible set of relationships for the six proposed species of *Homo*, according to the AR model. The data are the same as in Figure 11.1

Physical features we associate with modern humans eventually appeared everywhere but were manifested in different ways in different populations and in different environments. Thus, we are today and have always been a variable species—but a *single species*.

The African Replacement Model (AR) This model assumes that the different groups of fossils we discussed (or even more) are distinct species. Genus *Homo* began in Africa about 2 mya but during that time multiple branches have evolved, each eventually becoming extinct until the branch that gave rise to *Homo sapiens*, around 200,000 ya. Our species spread out and fairly quickly replaced any "archaic" species still around, presumably because our species was better adapted. Figure 11.43 is one proposed evolutionary tree for the six species of *Homo* we used to organize our discussion in this chapter.

The Evidence

There are four areas of evidence that can be brought to bear on this debate. Remember, for evidence to be relevant, it must distinguish between the models or suggest another one:

The Fossil Record This would seem to be the best area of evidence, since it represents the real phenotypic record of the evolution of our genus. And yet, the fossil record is ambiguous and thus inconclusive. Are the physical differences among the fossil groups enough to warrant placing them in separate species?

It really depends on what you *want* to find! If you think we are a distinct species then you will focus on the differences and translate them into species differences. If you feel all the groups are in the same, single species, then you'll see the differences as within an acceptable range of variation *within* a species.

One thing to note is that the groups of fossils do not show us the full story of variation through the last 2 million years. Look again at Figure 11.43 and note that there are big gaps among the groups such that most of the time is *not* represented by fossils. Thus, the fossil data are incomplete.

The Archaeological Record These data can also be used in support of either model. AR supporters find jumps in cultural sophistication and complexity, especially between the Neandertals (the typical species of comparison) and modern *Homo sapiens*. MRE supporters interpret the evidence to show gradual change. They note that culture, too, has to evolve, so that our relatively small sample of artifacts over time represents points on a continuum of culture change as our species got, simply put, better and better at using culture as our adaptive means. The archaeological record is thus also ambiguous and inconclusive.

Genetics Contrary to common opinion, much of the genetic evidence is also of no help in clearly distinguishing between the two models.The most striking thing about modern human genetic diversity is the lack of it. We are a very genetically homogeneous species (a topic we'll delve into more in Chapter 13).That fact could be accounted for if we are a young species, with not much time to accumulate genetic diversity. But it could also be accounted for if we are a very old species but a mobile one with extensive gene flow spreading around genetic variation.

The pattern of the genetic diversity that does exist in our species (Figure 11.44) shows greater diversity within sub-Saharan Africa than in the entire rest of the world, with the diversity of the rest of the world largely a subset

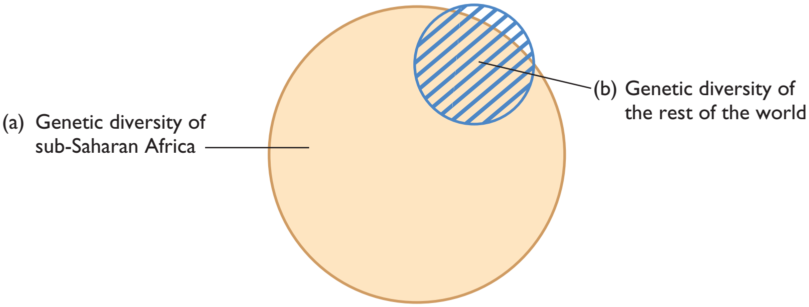

(a) Genetic diversity of sub-Saharan Africa
(b) Genetic diversity of the rest of the world

FIGURE 11.44 Comparative genetic diversity. Circle (*a*) represents the genetic diversity of humans from sub-Saharan Africa and (*b*) the genetic diversity of the rest of the world's peoples. Note that African diversity is much greater and that most of the diversity of the rest of the world is a subset of African diversity. (Circles are not drawn to scale.) par40005_

of African diversity. But this just tells us we are an African species, and that populations in the rest of the world were initially founded by a small, non-representative sample of Africans who happened to find their way off the continent over that one small northeastern strip of land. Both models acknowledge this scenario. The pattern doesn't say *when* our species evolved in Africa.

Finally, as we discussed in Chapter 9, genetic diversity can be translated into a "clock" to estimate when the divergence began. Most such calculations point to an origin of our genetic diversity at 150,000 to 200,000 ya. However, calculations can range more widely than that, and because different types and amounts of DNA are used there are differing results. There is disagreement over whether such studies are tracing the history of a species or simply the history of a particular lineage of DNA.

But what about DNA from fossils themselves? With new technologies we have been able to reconstruct the complete genome of three Neandertals from Croatia. Based on this reconstruction it appears that a small amount of the DNA of Europeans and Asians (1 percent to 4 percent) can be traced to Neandertals. This implies that there was interbreeding between *Homo sapiens* who left Africa and "archaic" populations already living in other areas of the Old World. Thus, by the standard definition, we and they are *not* different species. Some new DNA, from that finger bone found in Denisova Cave, Siberia, bears this out because of the specific similarities and differences between its genes and those of other living and ancient populations. More information will come as we are able to extract DNA from even older fossils (if that is possible).

And finally, some new studies (Gibbons 2011e) show evidence that there was interbreeding between *Homo sapiens* in Africa and some "archaic" populations. Again, if this is the case, it bolsters the idea of a single, interbreeding species showing variation through time and across space.

Evolutionary Theory This, to me, is the deciding factor, for a very simple reason. Remember that species evolve through profound isolation cutting off gene flow, with subsequent divergence of genomes and phenotypes to the point where interbreeding is no longer possible. Our genus, ever since it first appeared in Africa almost 2 million years ago, has been characterized by increasing mobility and the accompanying exchange of genes. We even have a proclivity for the activity that results in the exchange of genes (see Chapter 7). We also increasingly came to rely on culture as our major adaptive mechanism, thus limiting the extent to which we needed to genetically adapt to new and different environments. Simply put, could such a group of organisms have experienced the kind of profound isolation and change required of speciation *up to ten times* in 2 million years, as some would have it? I think not.

Thus, despite continuing arguments among anthropologists about the specifics, it looks as if there's a good possibility of at least *some* interbreeding among populations of genus *Homo*, as that genus spread around the world. A limited version of the MRE model is supported.

Is This Debate Important?

A good question; it sure seems to be if one looks at the strongly worded arguments from both sides. And it's a fun topic to argue about! Many words have been written and spoken. But it seems that at its core it's largely a philosophical issue. AR proponents seem adamant in assuming *Homo sapiens* is new and profoundly different from the other members of the genus. MRE proponents feel that evidence of species differences is beyond direct testing, so that the burden of proof is on the AR people.

Remember, to a great extent the names we give groups of organisms, especially those we can't directly test for the ability to interbreed, are our imposition on nature of our organizing principles. It seems to me best to look at genus *Homo* the way we looked at *Australopithecus*—focusing on the genus level and not arguing about the species question, which may be beyond a definitive answer. To be sure, some major changes have taken place in our evolution—at least they seem so to us, being the group in question!—but, stepping back, we can see that genus *Homo* as a whole can be meaningfully defined (see page 236) and we can view the last 2 million years as evolution within our anatomical and adaptive theme. We can say, for example, that "just about every way *Homo erectus* differs from its australopithecine ancestors also characterizes *Homo sapiens*. . ."(Wolpoff and Caspari 1997:256). And the recent genetic evidence for interbreeding clearly indicates a more complex evolution of our genus than either simply a straight line or a series of distinct branches, and we should focus on what happened, where, and when as we evolved.

SUMMARY

The record of the latest 2.5 million years of hominid evolution is complex. The fossils from the first 99 percent of this period are scarce, often fragmentary, scattered geographically, physically variable, and, in some cases, questionably dated. Not surprisingly, the interpretations of these fossils vary as greatly as do the fossils themselves. Our survey uses as a starting point the recognition of six species within genus *Homo* after the early *Homo* stage. I do not endorse this model but begin with it for the purpose of clearly organizing our discussion of a fairly complex topic.

The earliest species, *H. ergaster,* is found only in Kenya, but a possible branch of this group, *H. erectus,* spread through the rest of Africa and into Asia and possibly southern Europe. These two species are characterized by virtually modern postcranial skeletons, brain sizes close to and even overlapping the modern human range, and the invention of more sophisticated stone tools and other cultural innovations, including the use of fire. In Java, *H. erectus* may have persisted until as recently as 27,000 ya.

A geographically and chronologically scattered species, *Homo heidelbergensis,* appears next. The earliest examples of this group, from Spain, are placed by some authorities into a new species, *H. antecessor*. Located from England to South Africa to China, *H. heidelbergensis* displays brain sizes within the modern human range and at the modern human average, though their crania retain primitive features, giving them the label "archaic." They are known, starting about 200,000 ya, for the invention of the Levallois stone toolmaking technique—a sophisticated way of "mass producing" flake tools. They may have done some hunting as well.

The most famous of the "archaic" humans are the Neandertals, a separate species, *Homo neanderthalensis,* according to many. Living in Europe and Southwest Asia from 225,000 to 28,000 ya, this group exhibits traits that distinguish it from both *H. heidelbergensis* and later *H. sapiens*. These traits include a large, prognathous face, a ruggedly built skull, and a robust, muscular body—possibly adaptations to the cold glacial conditions many of their populations encountered. Neandertals are known for their retouched flake tools, which may have been used to carve bone and work wood, and for abstract cultural achievements such as burial of the dead and care of the elderly and infirm. They may also have been the first to haft stone points on wooden shafts.

Fossils transitional between archaic and modern *Homo* appear in Africa perhaps as early as 300,000 ya, and the first fully modern *Homo sapiens* are found in Africa and Southwest Asia beginning around 160,000 ya. From there, modern-appearing humans spread throughout the Old World and eventually to the islands of the Pacific and to the Americas. Archaic peoples—or archaic traits—disappear. During this time, big-game hunting develops, tool technology advances, sophisticated shelters are built, and humans create art.

Just how many species of genus *Homo* are we actually dealing with? And, how are all these groups related evolutionarily? These questions have been the source of sometimes intense debate but, while there is evidence for and against both points of view, the questions seem ultimately unanswerable and, thus, irrelevant to our overall evolutionary story.

QUESTIONS FOR FURTHER THOUGHT

1. Does it matter to *you* how many species of our genus have existed? Why or why not? Why do you think it matters so much to professional scientists?
2. The issue of whether groups of organisms are separate species within one genus or are variable populations within a single species has ramifications for living things other than hominids. One related topic is the Endangered Species Act. Why might this issue matter with regard to the implementation of that legislation?
3. What are the arguments in favor of lumping the Neandertals into *Homo sapiens*. What arguments might be made for splitting them into a separate species?
4. A little bit of science-fiction thinking: Suppose it was discovered that a population of *Homo floresiensis* still existed. What ethical questions would this bring up? How would your answer differ if they were a separate species or if they were members of *Homo sapiens* and thus capable of interbreeding with us?

KEY TERMS

Oldowan
core tools
flake tools
sagittal keel
torus
Pleistocene
glaciers
tundra
Acheulian technique
hand axe
bifacial
endocasts
postorbital constriction
Levallois technique
Mousterian technique
haft

SUGGESTED READINGS

For more on the Dmanisi finds, see a typically well-illustrated article in the August 2002 *National Geographic:* "New Find." See also "The Pathfinders," by Josh Fischman, in the April 2005 *National Geographic*. For more on the Atapuerca finds from Spain, see the also well-illustrated book *The First Europeans: Treasures from the Hills of Atapuerca*, published by Junta de Castilla y León.

An interesting article linking an increase in human brain size with dietary change is "Food for Thought," by William R. Leonard, in the December 2002 *Scientific American*. And for more on ancient cannibalism, see Tim D. White's "Once We Were Cannibals" in the August 2001 *Scientific American*.

For the fascinating story of Eugene Dubois and the discovery of "Java Man," see Pat Shipman's *The Man Who Found the Missing Link: Eugene Dubois and His Lifelong Quest to Prove Darwin Right*. The story of the missing "Peking Man" fossils is the topic of *The Search for Peking Man*, by C. Janus.

An interesting history of paleoanthropology is *Debating Humankind's Place in Nature, 1860–2000: The Nature of Paleoanthropology*, by Richard G. Delisle.

An interesting article on early art is "First Impressions," by Judith Thurman, in the 23 June 2008 *New Yorker*.

For more on the "Hobbits," see "The Littlest Human," by Kate Wong, in the February 2005 *Scientific American*, and "World of the Little People," by Mike Morwood et al., in the April 2005 *National Geographic*. For a recent summary of discussions about the identity of the "Hobbits" of Flores Island, see "When Hobbits (Slowly) Walked the Earth," by Elizabeth Culotta, in the 25 April 2008 *Science*.

For the argument that the "Hobbits" are very ancient hominids see "Five Years of *Homo floresiensis* by Leslie Aiello in the *American Journal of Physical Anthropology* Vol. 142, 2010.

There is extensive literature about the AR/MRE debate. I would especially recommend the two books by the major proponents of each point of view: *Race and Human Evolution: A Fatal Attraction*, by Milford Wolpoff and Rachel Caspari, in support of the MRE model, and *African Exodus: The Origins of Modern Humanity*, by Christopher Stringer and Robin McKie, in support of the AR model. The Wolpoff and Caspari book includes a good historical review of the issue. For an update see "A New View of the Birth of *Homo sapiens*" by Ann Gibbons in the 28 January, 2011 issue of *Science*.

12 CHAPTER

Evolution and Adaptation in Human Populations

From distant climes, o'er widespread seas
we come.
—George Barrington

We have followed the evolutionary history of the hominids up to *Homo sapiens* in its anatomically modern biological state. But the story of hominid evolution doesn't end just because we finally arrive at modern humans. The processes of evolution within a species, including our own, are continuous. A species undergoes change over time, even as it remains a single species.

All the processes of evolution have continued to operate, acting on the human "theme" and changing us over time and across geographic space. As we divided ourselves into groups based on ethnic identity, nationality, language, and religion, we provided those evolutionary processes with new and varying breeding populations. And because evolution takes place within populations, the nature of those cultural groups also affected the further evolution of our species as a whole. So did the behaviors—the cultural systems—of the people in those populations. Our biology and our culture are interrelated and affect one another.

As biological anthropologists, then, we are interested not only in how we evolved but also what we evolved into, how we continued to evolve over the recent past, and how we are evolving even today. Here, we will focus on two subjects that relate to what we've been discussing throughout the book so far: adaptation to environments in general and adaptation to other organisms—in particular, to those that cause disease. In this chapter, we will address these questions:

How are all members of our species adapted to environmental variables?

How have we humans adapted to the specific environments in which we live?

Are all human phenotypic variations adaptive?

How have diseases affected human evolution and human populations?

POPULATION ADAPTATIONS

Living human populations inhabit every continent except Antarctica and we have to deal with nearly every imaginable set of environmental circumstances the earth presents. We have been doing this for just about as long as *Homo sapiens* has existed and even at the beginning of our genus, 2 mya, humans successfully moved into a wide range of environments.

One would expect, therefore, that different populations of our species would be differently adapted to those various environments. Obviously, most of our adaptations are cultural. We build shelters, manufacture clothing, make tools, and invent various technological devices that are specifically geared to the environmental conditions with which we have to contend (Figure 12.1).

Human populations also differ in their physical appearance and in features of their physiology. Our species displays variations in phenotypic traits that are the results of genetic variation. Are some of these variable traits adaptive responses to different environments?

Species Adaptations

As members of the same species, all humans share many adaptations to variable conditions (see Beall and Steegmann 2000 for a detailed discussion).

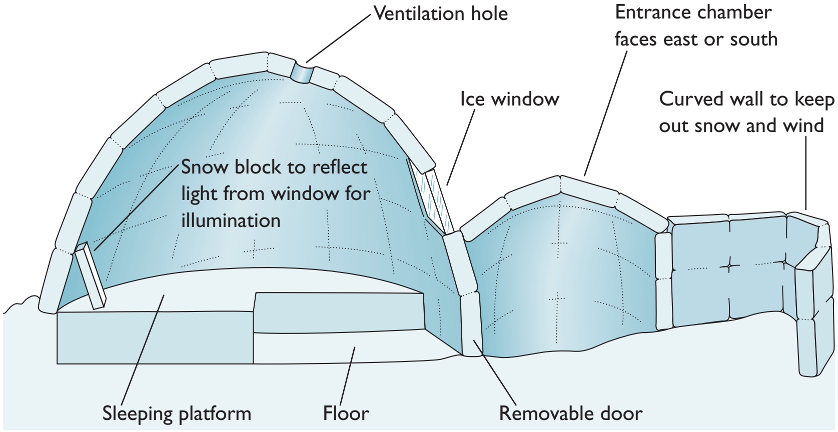

Ventilation hole
Entrance chamber faces east or south
Ice window
Curved wall to keep out snow and wind
Snow block to reflect light from window for illumination
Sleeping platform
Floor
Removable door

FIGURE 12.1
Cultural adaptation. The famous igloo of the Inuit has many ingenious features that make it remarkably adapted to life in a harsh climate.

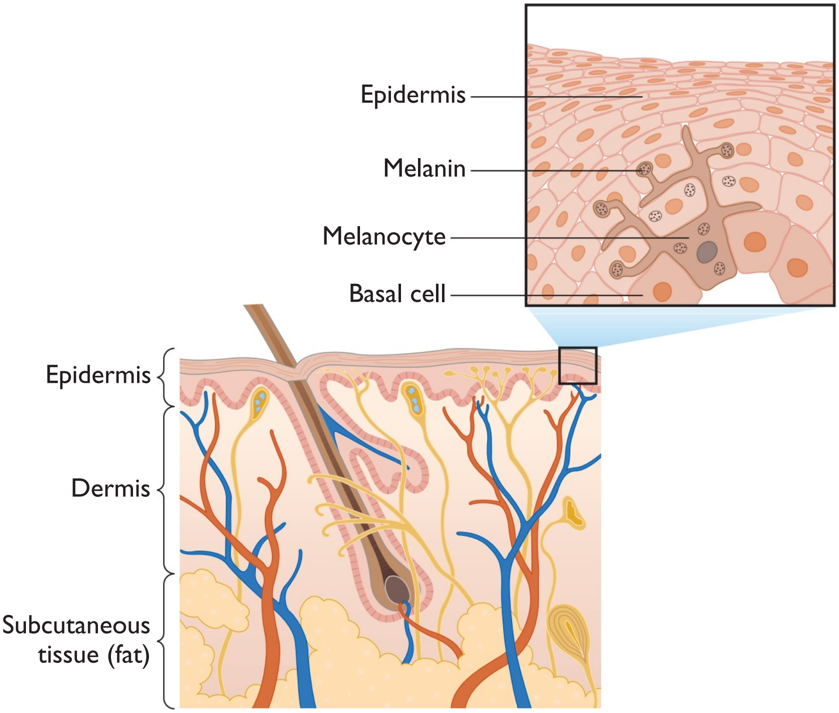


FIGURE 12.2
Melanocytes are located between the two top layers of skin. Melanin production varies with, among other factors, UV radiation exposure.

One important environmental variable is temperature. All humans sweat as a means of dissipating heat from the body. Our relative hairlessness may be an adaptation to promote the quick evaporation of sweat. Alternatively, when it becomes too cold, we shiver, our metabolic rate increases, and our blood vessels alternately widen and narrow to increase or decrease the flow of blood to warm various body parts as needed.

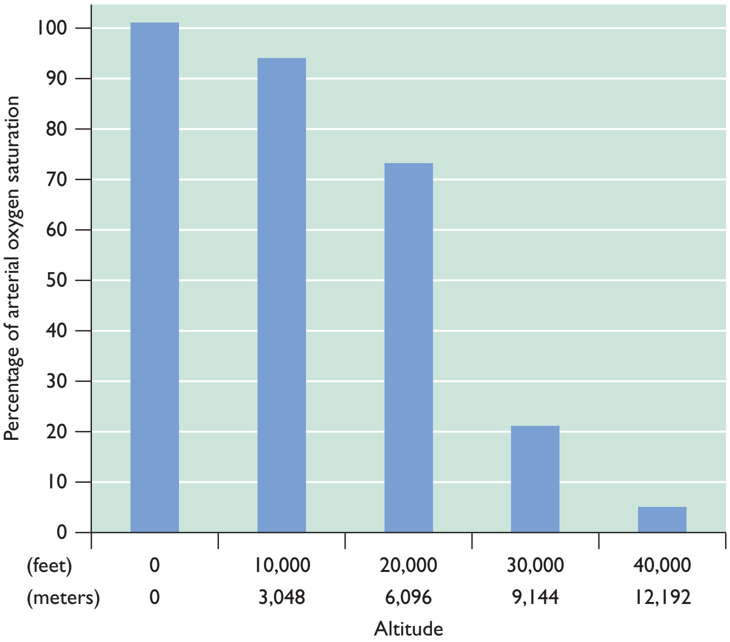
Similarly, we are all exposed to ultraviolet radiation from the sun. An excess of UV radiation can damage skin cells, alter the cells' DNA (thereby causing skin cancer), and adversely affect the body's immune system. Excess UV radiation can also break down folate, a chemical necessary for normal embryo development and sperm production. To protect tissues from UV damage, specialized skin cells called **melanocytes** produce the pigment **melanin,** a protein, and deliver it to the upper layer of skin, where it absorbs UV radiation (Figure 12.2). Melanocytes respond to increased UV levels by increasing their melanin production and darkening the skin. This, of course, is tanning. Even dark-skinned individuals can exhibit a tanning response.

Humans are also exposed to varying levels of oxygen. At high altitudes, oxygen concentration is lower, and low oxygen levels can have

melanocytes Specialized skin cells that produce the pigment melanin.

melanin The pigment largely responsible for human skin color.

FIGURE 12.3
The relationship between arterial oxygen saturation and altitude.
(Data from Frisancho 1993:223; Relethford 2008)



damaging, even deadly, effects on the human body (Figure 12.3). All humans, however, have some ability to respond biologically to this condition. After a time at higher-than-normal altitudes, a person's respiratory and heart rate will increase, as will one's red blood cell count. Hemoglobin concentration may go up as well. All this helps the body better acquire and use what oxygen is available.

Variation in Adaptations

Humans have settled in places from the hottest deserts and rain forests to the coldest reaches above the Arctic Circle. No matter how much we may sweat, shiver, increase our metabolic rate, and change the shape of our blood vessels, it may not be enough to deal with some environmental extremes. Thus, populations have undergone natural selection for genetic and phenotypic variation in response to certain environmental variables. Here are some classic examples.

Climate Populations that inhabit hot climates tend to be linear in build, and those in cold areas tend to be stockier (Figure 12.4). This is because

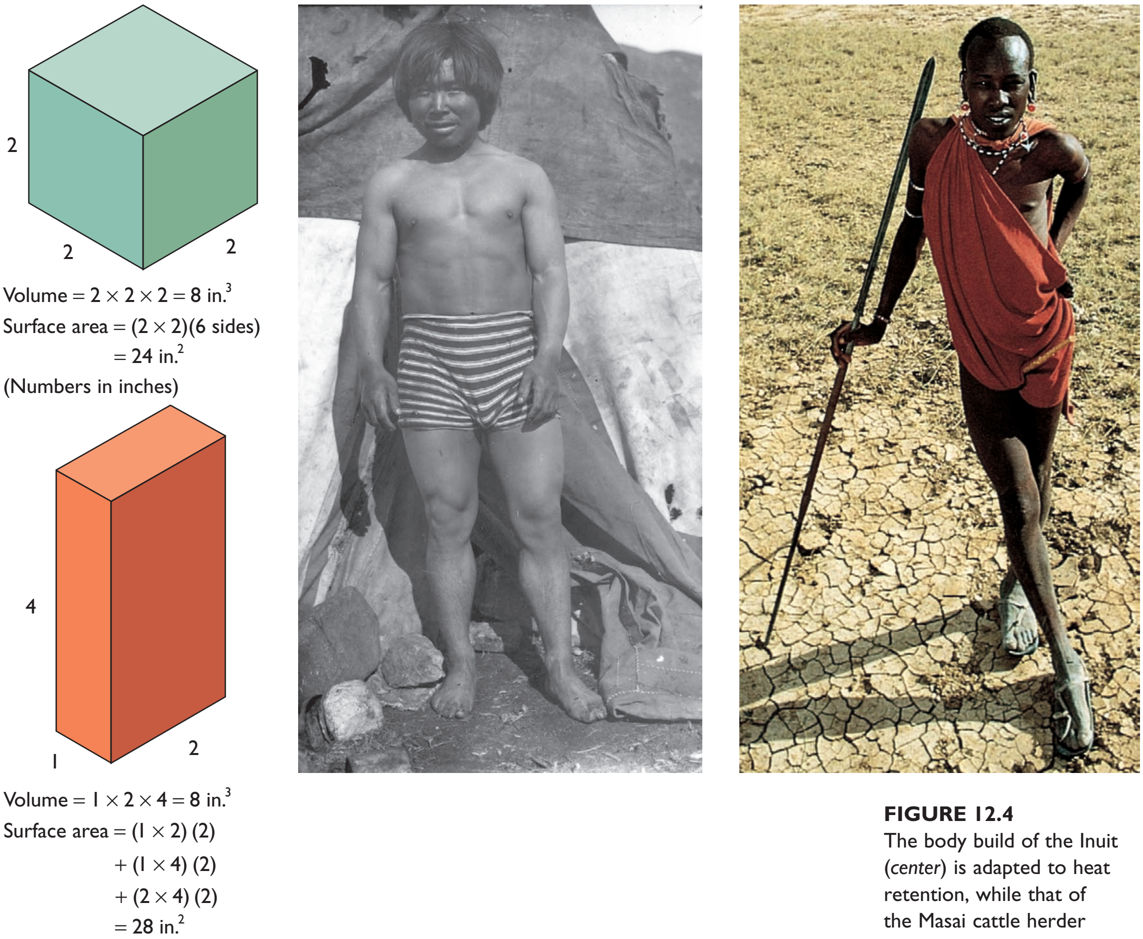

2
2
2
Volume = 2 × 2 × 2 = 8 in.^{3}
Surface area = (2 × 2)(6 sides)
= 24 in.^{2}
(Numbers in inches)
4
1
2
Volume = 1 × 2 × 4 = 8 in.^{3}
Surface area = (1 × 2) (2)
+ (1 × 4) (2)
+ (2 × 4) (2)
= 28 in.^{2}

FIGURE 12.4
The body build of the Inuit (*center*) is adapted to heat retention, while that of the Masai cattle herder from Kenya (*right*) is built to promote heat loss. The relationship between surface area and shape for two solids of equal volume (*left*) explains the adaptations of the two men pictured.

the linear individual has a greater surface area and so loses heat more rapidly, whereas the stockier person has a smaller surface area and so retains heat better.

A similar relationship holds true for head shape, which was a popular measure of racial affiliation in the nineteenth and early twentieth centuries. As it turns out, there is a correlation between head shape and climate. Simply put, populations in cold climates tend to have wider heads relative to their length. Rounded heads lose heat more slowly.

Nose shape is another example. The mucous membranes inside our noses serve to warm and moisten air. Cold and dry air is detrimental to the lungs and to the mucous membranes themselves. Thus, long, narrow noses

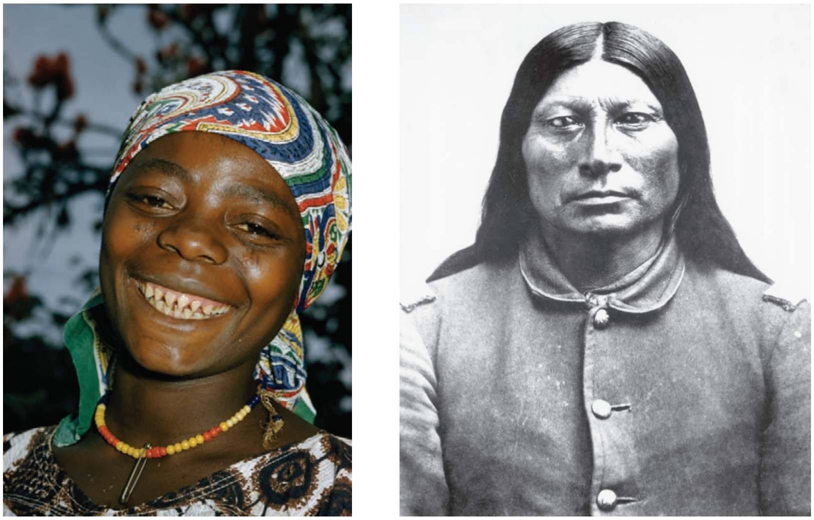


FIGURE 12.5
(*left*) A woman from the rain forests of the Republic of the Congo with a short, broad nose. (*right*) A Northern Arapaho (1884) with a long, narrow nose. His name, in fact, is Ta-Quo-Wi, "Sharp Nose."

are found in populations in cold and/or dry climates. Short, wide noses are more common in hot and/or moist areas, where the air does not need to be adjusted as we breathe in (Figure 12.5).

Sunlight Ultraviolet radiation varies with latitude. Sunlight strikes the earth more directly at the equator and at an increasingly greater angle the farther one gets from the equator. The greater the angle, the more atmosphere the solar radiation must travel through. Thus, more UV radiation is absorbed by ozone in northern latitudes. Not only do humans have the ability to tan in response to increased UV levels, but, as is obvious to us all, populations are genetically programmed for differences in skin color, and these differences also vary by latitude (Figure 12.6). In general, populations closer to the equator have darker skin, and those farther away from the equator have lighter skin (Figure 12.7). It is generally agreed that the relationship between dark skin and high levels of UV radiation is an example of an adaptive response (Beall and Steegmann 2000; Chaplin 2004; Jablonski and Chaplin 2000, 2002; Parra 2007). Because of the damaging effects of UV radiation, particularly destruction of folic acid necessary for embryo development and sperm production, populations at or near the equator have undergone selection for permanently higher levels of melanin production. Darker-skinned people do not have more melanocytes than lighter-skinned ones, just more melanin production. An implication of this, of course, is that dark skin was the original human skin color, since our species first evolved in equatorial Africa. Moreover, the African

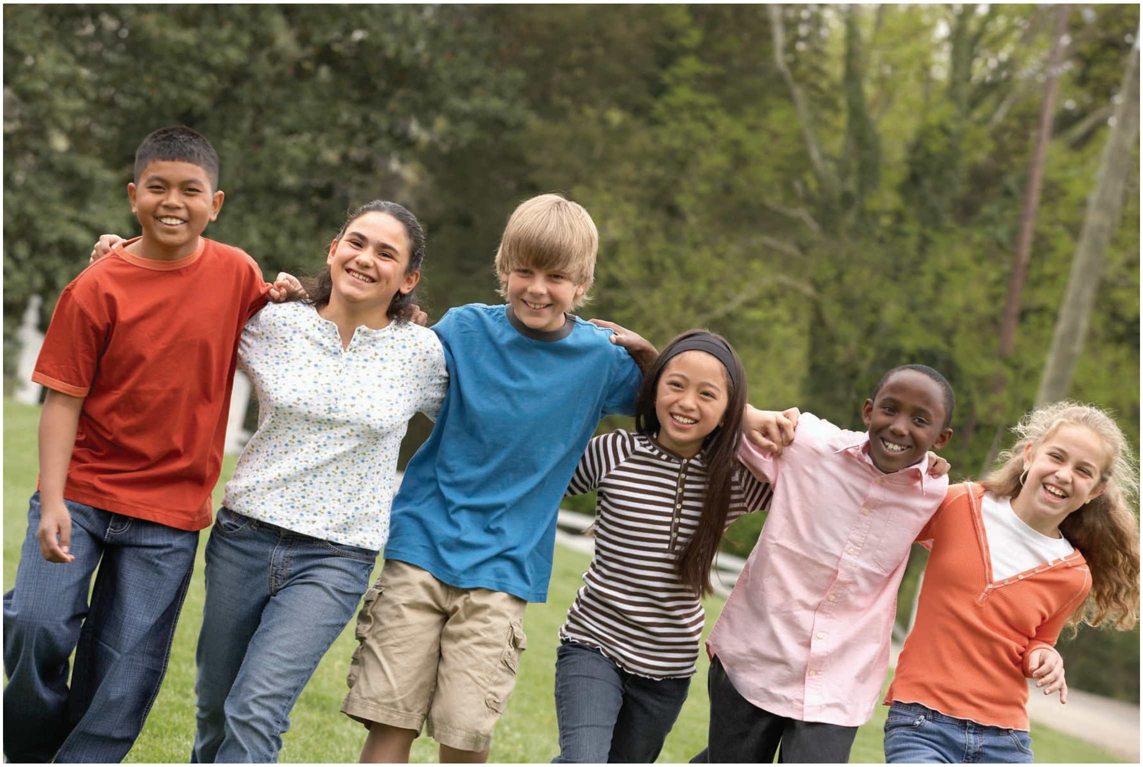


FIGURE 12.6
Human skin color ranges, in a continuum, from very dark to very light.

great apes, our closest relatives, have darkly pigmented skin, so it could be a shared trait inherited from a common ancestor. The adaptation would have become even more important when hominids lost their protective covering of hair.

The question then becomes, Why did populations who moved away from the equator evolve lower melanin production and therefore lighter skin? It is easiest to say that since dark skin was no longer needed, it became light. Evolution, however, doesn't really work this way. More likely, there was an adaptive reason why lighter skin was actively selected *for*.

The explanation has to do with vitamin D production. Vitamin D can be synthesized by the body in the lower layers of skin when a precursor of the vitamin is activated by UV radiation. This vitamin is important in regulating the absorption of calcium and its inclusion in the manufacture of bone. This is especially important during pregnancy and lactation, possibly accounting for the fact that in all populations females tend to be more lightly

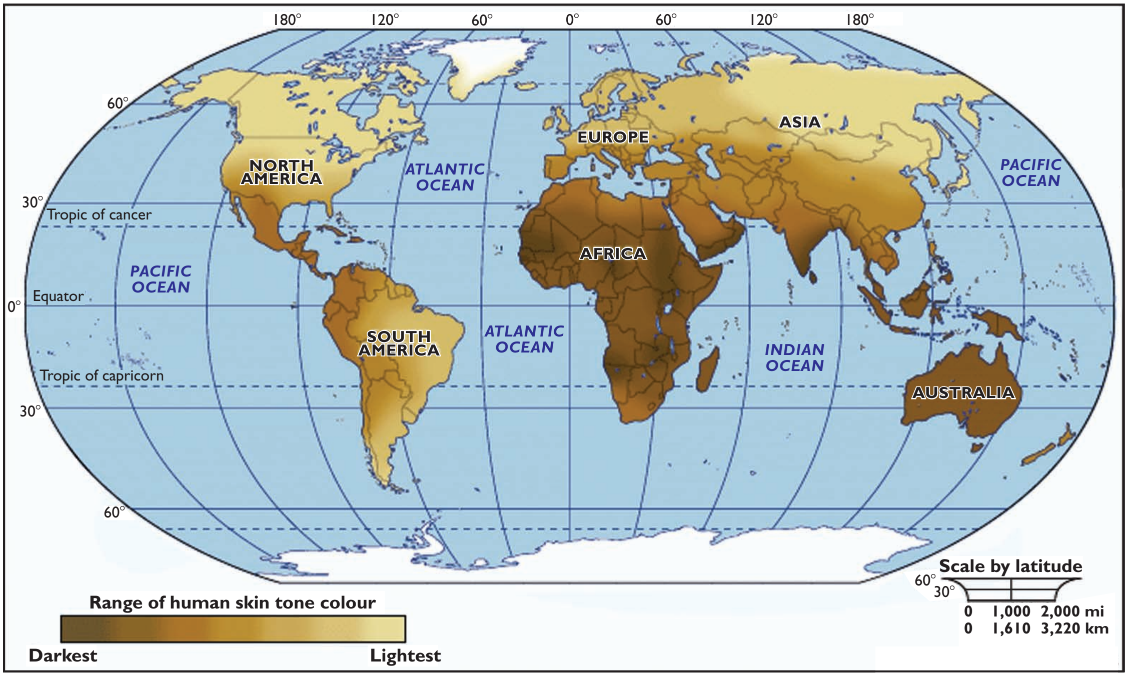

180°
120°
60°
0°
60°
120°
180°
60°
30°
Tropic of cancer
Equator
0°
Tropic of capricorn
30°
60°
NORTH AMERICA
SOUTH AMERICA
EUROPE
ASIA
AFRICA
AUSTRALIA
ATLANTIC OCEAN
PACIFIC OCEAN
ATLANTIC OCEAN
INDIAN OCEAN
PACIFIC OCEAN
Scale by latitude
60°
30°
0 1,000 2,000 mi
0 1,610 3,220 km
Range of human skin tone colour
Darkest
Lightest

FIGURE 12.7
Skin color distribution around the world. Darker skin is concentrated in equatorial regions. Note that the gradation is gradual across geographic space (a topic we'll take up in detail in Chapter 13).

pigmented than males (Jablonski and Chaplin 2000, 2002). Deficiency in vitamin D can lead to a condition of skeletal deformity in children known as rickets. (There is an adult version of the abnormality as well.) Bones with rickets are also more prone to breakage, and the disease can cause a deformity of the pelvis that can make childbirth difficult. Vitamin D is also important for the normal functioning of the immune system.

As populations moved away from the equator, those with darker skin could not manufacture sufficient vitamin D for normal bone growth and maintenance and immune-system functioning. Those with lighter skin, therefore, were at an adaptive and, thus, a reproductive advantage. Over time, lighter skin became the normal, inherited condition in these groups. Skin color is thus seen as a balancing act—dark enough to protect from the damaging effects of UV radiation and light enough to allow the beneficial effects.

Diet Culture is part of our environment, and thus natural selection can take place in response to cultural practices. One example involves variation in the body's ability to produce lactase, an enzyme necessary for the digestion of lactose, a sugar found in milk. For the majority of people, the ability to digest milk decreases after childhood. For them, ingesting dairy products can result in digestive problems such as diarrhea and cramps.

Populations with long histories of extensive reliance on dairy farming, however, have high frequencies of *lactase persistence*, the ability to produce lactase beyond childhood. The dominant allele of a single gene that codes for lactase persistence has been selected for because those possessing that allele had an advantage—the ability to use an important dietary resource throughout their lives. This gene is common in Europeans and among the Fulani, cattle herders of West Africa, who rely heavily on milk in their diet. Analysis has indicated that this selection has taken place over the last 5,000 to 10,000 years, which is consistent with estimates of the origin of dairy farming.

There is also evidence of some relationship between lactase persistence and latitude. Recall the information about vitamin D and latitude just discussed. Perhaps increased ability to digest lactose in northerly latitudes is advantageous because lactose aids in calcium absorption. This might help explain the high frequencies of lactase persistence in Europeans (as much as 96 percent in Swedes), but it doesn't account for high frequencies in the Fulani.

These examples demonstrate that our species, despite its ability to adapt through culture to a wide array of environments, has still undergone natural selection for and against certain features in response to those environments. The adaptation of sickle cell anemia in malarial areas is another example (see Chapter 4). Although we might like to think we have buffered ourselves against the processes of evolution, natural selection has occurred in modern *Homo sapiens*, and it continues to affect us.

Are All Variations Adaptively Important?

We can see in the distribution of physical and physiological traits (such as body build and features, skin color, and lactase production) some obvious correlations with environmental factors that lead us directly to our conclusions about the adaptive significance of these variable traits. Other variable traits, on the other hand, seem distributed among our populations in such a way that there is no obvious relationship to environmental circumstances.

The distribution of blood types in the ABO system (see Chapter 3) is a perfect example of a variation with no obvious relationship to the environment (Figure 12.8), no reason to how the various frequencies of the phenotypes are dispersed around the world. Type A, for example, is

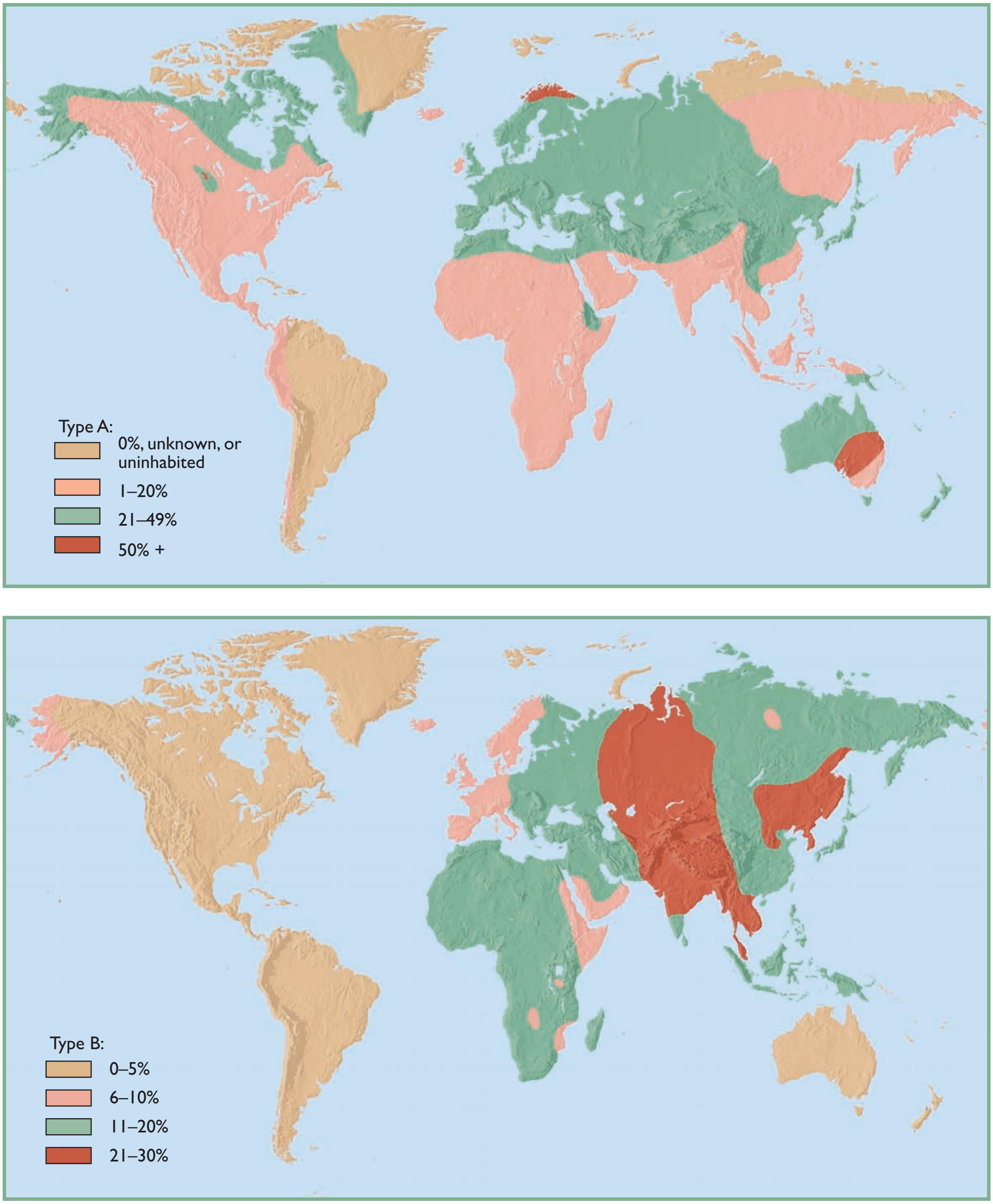

Type A:
0%, unknown, or uninhabited
1–20%
21–49%
50% +
Type B:
0–5%
6–10%
11–20%
21–30%

FIGURE 12.8
These maps show the approximate frequency distributions of type A and type B blood, demonstrating the lack of an obvious explanation in the distribution of this variation. (The categories here are arbitrary. The blood-group frequencies in reality vary gradually across geographic space.)

totally absent among some native South American groups but is found in frequencies of over 50 percent in parts of Europe and native Australia. Type B, although found in moderate to high percentages in Asia, is nearly absent among Native Americans, who originated from Asian migrants. Type B is also nearly totally absent in Australia but is found in moderate percentages in New Guinea. Type O, the most common in the species, still ranges from 40 percent in parts of Asia to 100 percent among some native South Americans.

Are the variations of this genetic trait adaptively neutral? Scientists believe this to be the case for some other blood-group systems. (There are about thirty different blood-group systems besides the ABO system, different chemical phenotypes in the blood that are the results of different genes with multiple alleles.)

The phenotypic trait involved in the ABO system is the presence or absence of certain proteins, called **antigens,** on the surface of the red blood cells. In addition, from shortly after birth your blood plasma contains other proteins, or **antibodies,** that react against the alternate version of your antigen. For example, the alternate version of antigen A is antigen B. Table 12.1 shows how these are expressed in the ABO system. The reactions between antigens and antibodies are the reason that blood used for transfusions must match the blood type of the recipient.

Since antibodies of various sorts are important components of our bodies' immunological system, disease is one obvious factor to examine for an adaptive significance of the ABO variation. Some microorganisms possess antigens that are similar to the A and B antigens, so perhaps certain blood types are predisposed to fight off certain infectious diseases. At the same time, if an infecting microorganism possesses antigens that are similar to your own, then your system may not be stimulated to produce the proper antibodies against the organism, making you more susceptible to that disease.

antigens Substances, such as proteins, that can trigger an immune response, for example, the production of an antibody.

antibodies Proteins in the immune system that react to foreign antigens.

TABLE 12.1
ABO Blood Group Phenotypes and Antibodies

Genotypes	*Phenotypes*	*Antigens*	*Antibodies*
AA AO	A	A	anti-B
BB BO	B	B	anti-A
AB	AB	A, B	none
OO	O	none	anti-A, anti-B

Some correlations between blood type and susceptibility to diseases have been suggested. Type A has been statistically associated with bronchial pneumonia, smallpox, and typhoid; type O has shown correlations with bubonic plague. Among the data that support some connections among these factors is the low frequency of type O in India, where there is a long history of frequent plague epidemics.

There is some evidence that mosquitoes are more attracted to type O persons. If so, then diseases carried by mosquitoes, such as malaria, would also be influenced, although indirectly, by blood type.

There are correlations as well between blood types and noninfectious gastrointestinal diseases. Type O persons appear to have a greater chance of duodenal and stomach ulcers and type A persons of stomach cancer. Most people have blood-group antigens in their body fluids, including their gastric juices, as well as in their blood, and so there may well be some reactions between these antigens and chemicals in the food one eats.

Along the same lines, there may also be reactions between blood antigens in the digestive tract and some intestinal bacteria. Individuals of certain blood types may be more or less affected by bacterial ailments such as infant diarrhea.

What do blood-type correlations tell us? Certainly these data indicate that a selective role for the ABO system is possible, especially with diseases that affect people during or before their reproductive years. We must demonstrate, however, that selection is, in fact, taking place. The fact that we have gained control over some of the diseases in question limits our ability to study them in the present, and so we have to rely, as with the plague connection, on historical records.

Moreover, we must establish a cause-and-effect relationship between antigen and disease, and we must also show if, and under what conditions, this would make enough of a difference to affect reproductive success. The ABO system is also found in some other primates, so the origin of the variation itself may be hidden in our evolutionary past. Some of the more important connections are with diseases of dense urban populations. Thus, selection for certain blood types, and their distribution, may be a fairly recent phenomenon.

As this single example shows, the topic is a complex one. We asked at the beginning of this section, Are all variable traits adaptively important? The answer is, we don't know for sure. Human variations need to be examined for their selective contributions to populations within the species. We may find, however, that some of our variable traits make no difference at all—or at least make no difference now.

DISEASE AND HUMAN POPULATIONS

Diseases Are "Natural"

We tend to think of diseases as abnormalities—and for individuals suffering from them, they are. But diseases are as much a part of life as any other aspect of our biological world. Many diseases are caused by other living organisms—viruses, bacteria, and protozoa—and are carried by other species, they are really perfectly natural. Disease-causing species have adapted to the biology of their hosts, and the hosts at least attempt to adapt to the disease-causing species.

Diseases can also have wide-ranging effects on population size and structure. In fourteenth-century Europe, a drop in population was the result of plague, mostly bubonic plague, a fatal bacterial disease carried by fleas, which were in turn transported by rats. A major outbreak began in Italy in 1347 and spread rapidly across Europe over the next five years, killing 25 million people. The period came to be known as the Black Death (Figure 12.9). The fact that it took longer to replace the 25 million than to kill them off results from two facts. First, there were further, though smaller, outbreaks of plague over the next century that kept the death rates high. Second, a phenomenal growth rate of around 100 persons per thousand would have been required each year to restore the population in five years. (*Growth rate* is birth rate minus death rate.) By comparison, the U.S. growth rate in July 2011 was only 5.45 persons per thousand.

Bubonic plague spread so quickly through Europe during those years because of the dense populations of its cities and the extensive trade networks that linked them. Rats that carried the fleas moved easily from place to place, and the bacteria easily moved from person to person. Culture affected a biological event—and vice versa. Many aspects of European culture were affected by the Black Death—from economy to art to religious dissent and reform movements (Figure 12.10).

We tend to think that our species, especially in modern times, has removed itself from many, if not most, such relationships. After all, those of us in developed countries virtually ignore some diseases that a generation ago were serious threats. Polio (still a problem during my childhood) has been virtually eliminated from the United States and Europe. Tuberculosis is rare in the United States, as is measles. In 1980 smallpox was declared eradicated worldwide. In the United States, only one of the eleven most common causes of death (pneumonia/influenza) is an infectious disease (Figure 12.11).

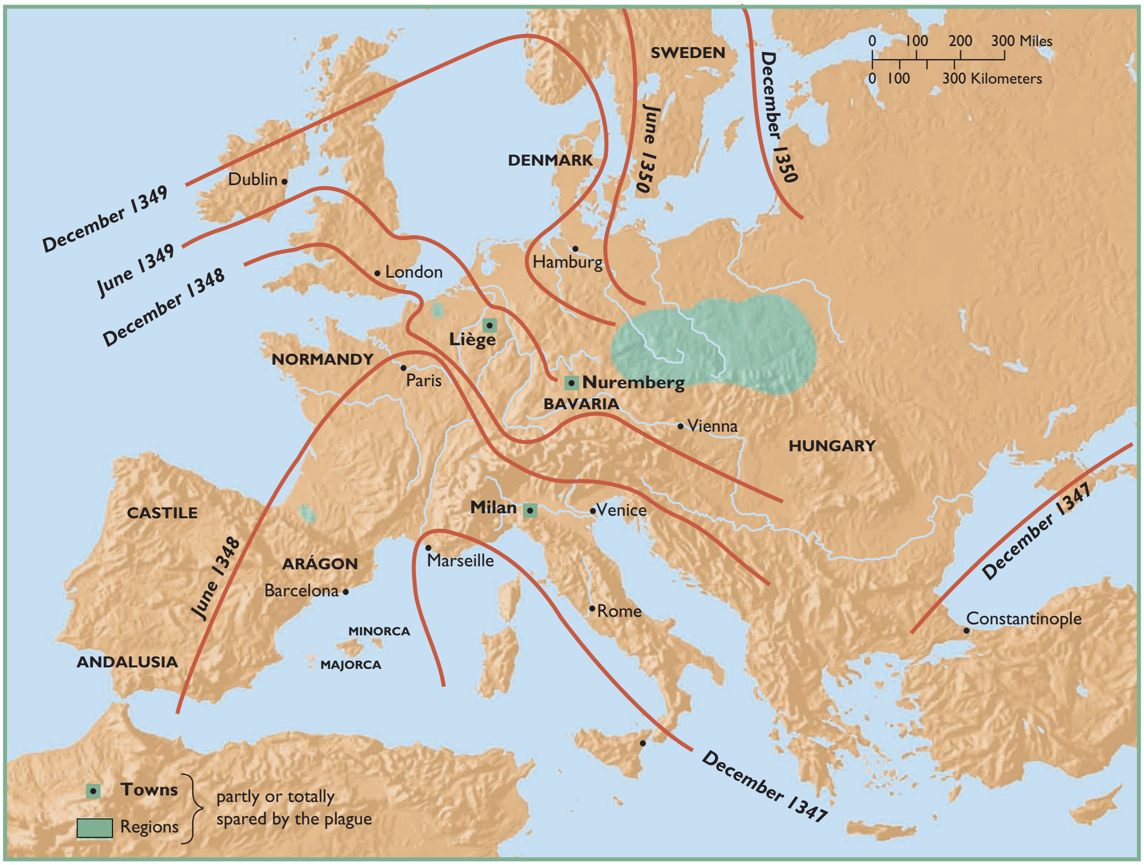

SWEDEN
June 1350
December 1350
0 100 200 300 Miles
0 100 300 Kilometers
DENMARK
Dublin
December 1349
June 1349
December 1348
London
Hamburg
Liège
NORMANDY
Paris
Nuremberg
BAVARIA
Vienna
HUNGARY
CASTILE
Milan
Venice
December 1347
June 1348
ARÁGON
Barcelona
Marseille
Rome
MINORCA
MAJORCA
Constantinople
ANDALUSIA
December 1347
Towns
Regions
partly or totally spared by the plague

FIGURE 12.9
This map shows the progression across fourteenth-century Europe of the Black Death, an event that killed over one-third of Europe's people in only five years.

But there are still diseases that disable and kill us, and new diseases or new strains of old diseases are even now emerging as the species that cause them continue to undergo the processes of evolution. We have already discussed the examples of sickle cell anemia, malaria, and plague, and there may well be evolutionary relationships between our blood types and certain diseases. Diseases are significant factors of natural selection.

Disease and Hominid Evolution

Evolutionary relationships among human and animal viruses suggest that some viruses have even played a role in hominid evolution (Van Blerkom 2003). As major causes of illness and death, viruses can be agents of

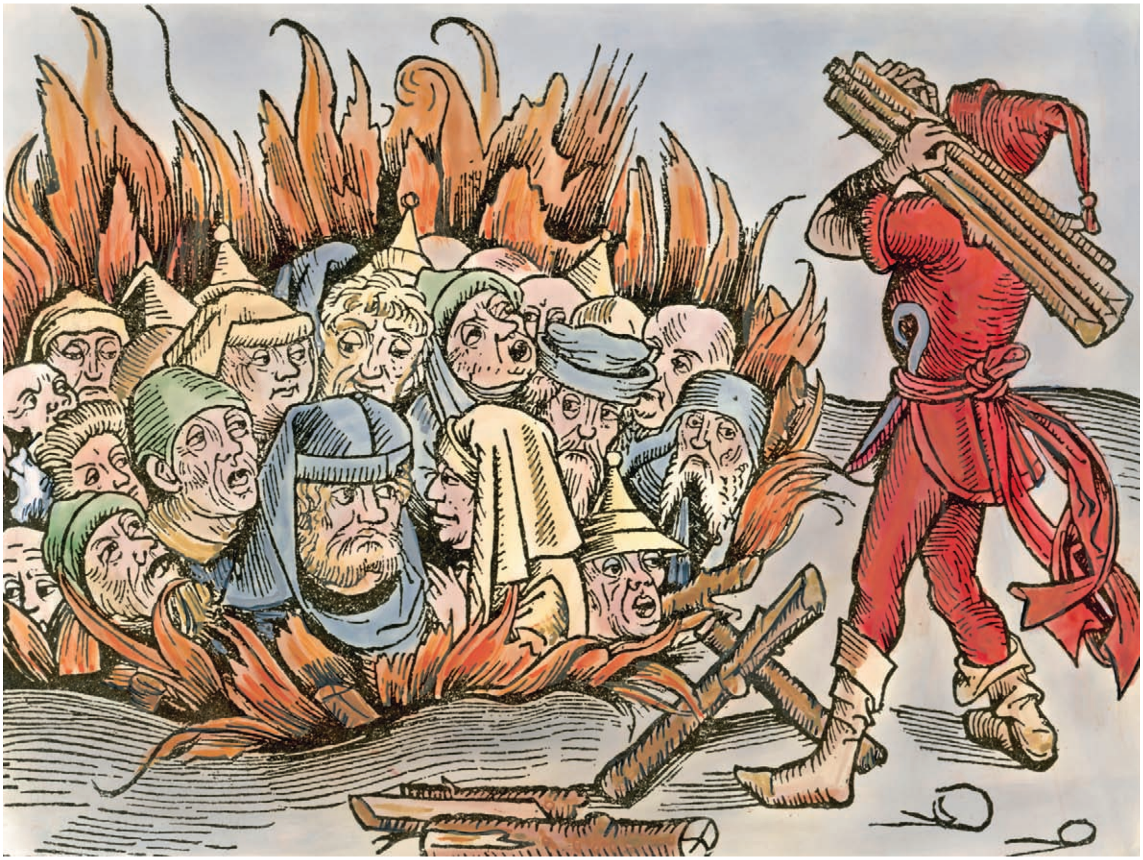


FIGURE 12.10 An illustration from Boccaccio's *The Decameron* (1353) showing Jews being burned because it was thought they were responsible for the plague.

selection within populations—for example, selecting for and maintaining general diversity in the all-important human immune system.

Viruses can also be involved in selection between populations accounting for the extinction of individual populations. Perhaps early migrants out of Africa—where populations had a long time to develop immunities to certain diseases—carried pathogens to hosts who lacked immunity. An analogous phenomenon occurred, for example, when the Spaniards conquered the Aztecs of Mexico in 1521. European diseases—smallpox, measles, and influenza—to which the Aztecs had no prior exposure and thus no immunity, probably did more to lead to their downfall than did the military actions of the Spanish soldiers.

Finally, since viruses operate by commandeering host-cell machinery for their own purposes, some may also have played a more direct role in

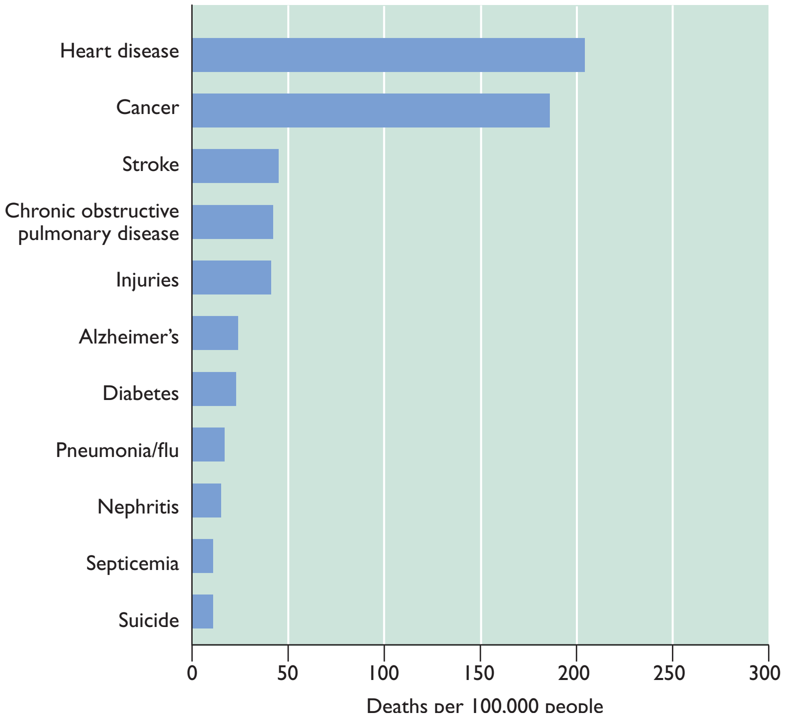


FIGURE 12.11
The eleven leading causes of death in the United States in 2005. Note that only one (pneumonia/flu) is infectious.
(Source: National Center for Health Statistics 2005)

altering the human genome and thus, perhaps, in accounting for some of the evolutionary changes seen in hominid history (Van Blerkom 2003). Remnants of ancient viruses make up about 1 percent of the human genome. Some of these viral sequences may cause pathological conditions, but others, after millions of years of evolution, may be involved in such normal processes as placental formation and fetal development. An evolutionary tree of certain related virus types mirrors the evolutionary tree of their host species. This is evidence of a long-term coevolution.

Disease and Human History

Looked at from the biocultural perspective we have used throughout this book, we may see general trends in the relationship between diseases and the human species. Anthropologist George Armelagos (1998; Armelagos et al. 1996) has outlined these trends and refers to them as three "**epidemiological** transitions."

epidemiological Pertaining to the study of disease outbreaks and epidemics.

For most of our species' history, we lived in small, widely dispersed, nomadic foraging groups. Our ancestors certainly experienced diseases of various sorts and would have come into contact with new diseases as they migrated to new environments. But infectious diseases may not have had serious effects on large numbers of people or many different populations, since they would have had little chance of being passed on to many other humans.

First Epidemiological Transition When some people began to settle down and produce their food through farming and animal domestication—starting about 10,000 ya—the *first epidemiological transition* occurred. Infectious diseases increased in impact, as larger and denser concentrations of people provided the disease vectors with greater opportunity to be passed from host to host. Animal domestication brought people into contact with new diseases. Working the soil exposed farmers to insects and other pathogens. Sanitation problems caused by larger, more sedentary populations would have transmitted parasitic diseases in human waste, as would the use of animal dung for fertilizer. Agriculture also led to a narrowing of food sources, as compared with the varied diets of foragers which resulted in nutritional deficiencies. The storage of food surpluses attracted new disease carriers such as insects and rats. Trade between settled communities, as we saw in the case of the Black Death in Europe, helped spread diseases over large geographic areas. Epidemics, diseases that affect a large number of populations at the same time, were essentially nonexistent until the Agricultural Revolution.

Second Epidemiological Transition Beginning in the last years of the nineteenth century and continuing into the twentieth, we experienced the *second epidemiological transition*. With modern medical science providing immunizations and antibiotics and with better public health measures and improved nutrition, many infectious diseases were brought under control or even, as with smallpox, eliminated. There was a shift to chronic, degenerative diseases such as cancers and cardiac, circulatory, and pulmonary diseases. Fewer people were dying from infectious diseases and more were living longer. But the results of modern lifestyles in developed countries and among the upper classes of developing countries led to a more sedentary life leading to less physical activity; more stress; environmental pollution; diets contributing to obesity, clogged arteries, and diabetes; and smoking and alcohol consumption.

Third Epidemiological Transition But on the heels of the second transition has come the *third epidemiological transition*, and we are in it now. New diseases are emerging, and old ones are returning. Both of these phenomena can be understood in terms of evolutionary theory.

Contemporary Reflections

Are There Jewish Diseases? Are There Black Pharmaceuticals?

One could sarcastically respond that, no, diseases don't have religions, nor do drugs have skin colors. In fact, it wouldn't be such a sarcastic answer.

The basis of the question is the statistical correlation between certain groups and certain diseases. Indeed, there are a number of diseases—most famously Tay-Sachs disease (a lethal genetic disorder that destroys a person's nervous system in childhood)—associated with Eastern European (Ashkenazic) Jews. Sickle-cell anemia (see Chapter 4) is commonly associated with Africans and African Americans. Ellis–van Creveld syndrome (a genetic disorder that affects bone growth) is found more often in Old Order Amish from Pennsylvania than anyone else.

So, does that mean that being Jewish gives one an increased chance of experiencing the rare mutation? Is Tay-Sachs a "Jewish disease?" Recall the explanation for sickle-cell anemia. The mutation can occur in anyone. It is found in highest frequencies in parts of Africa because of the prevalence of malaria there and because being heterozygous for sickle-cell confers a resistance to often-fatal malaria (and heterozygotes don't suffer a lethal form of sickle-cell). Thus, being African, or African American, does not *cause* the disease. Parts of Africa have low frequencies. A confluence of many factors simply made Africans and, by extension, African Americans, *statistically more likely* to have it.

The same is true for Tay-Sachs. It seems being heterozygous for this recessive allele confers a resistance to tuberculosis (TB), a disease that was a major cause of death in European cities into the twentieth century. Jews, for a thousand years, were confined to restricted, small, and crowded areas

The return of old diseases is the result of the fact that microorganisms are evolving species themselves. For example, new and serious antibiotic-resistant strains of tuberculosis have recently appeared. This evolution may have been encouraged by what some authorities consider our overuse of antibiotics, giving microorganisms a greater chance to evolve resistance by exposing them to a constant barrage of selective challenges. Some bacteria reproduce *hourly*, and so the processes of mutation and natural selection are speeded up in these species.

Emerging Diseases

Emerging diseases are also the results of human activity in the modern world, which brings more people into contact with more diseases, some of which were unheard of even a few decades ago. As people and their products become more mobile, and as our populations spread into previously little-inhabited areas, cutting down forests and otherwise altering of those cities (the origin of the term *ghetto*), where TB must have been even more rampant. Thus, a potentially lethal genetic disorder, which in one form aided in fighting a major infectious disease, accumulated in frequency, to the point where it was statistically associated with a certain group. (Genetic screening for carriers of the gene, giving potential parents vital information and a choice, has all but eradicated the disease among that group. Of ten babies born in North America with Tay-Sachs in 2003, none were Jewish.)

A reasonable explanation for the prevalence of Ellis–van Creveld among the Amish is the founder effect. By chance some of the founders of that population were carriers and, because the Amish are endogamous (marriage within), the allele accumulated in frequency.

At the same time, however, there are genetic differences around the world, some of which might have ramifications for health issues, specifically for pharmaceutical treatments. Not every drug works the same for everyone. Based on the common perception (which we will address in the next chapter) that biological racial groups exist and that they can be characterized by genetic differences, drug companies have marketed drugs specifically for whites or for blacks. This is what Jonathan Marks (2009:247) calls "racial pharmacogenomics," where "people are prescribed medications on the basis of census categories instead of their actual genetic makeup." The problem here is that even if some population differences in genetics exist that might relate to the efficacy of certain medications, it's not the case that, say, *every* black person has that genetic makeup. People categorized as black (or any other racial group) display genetic diversity. At best, it's the case that more (but not all) black people have some genetic expression than do members of other groups. So the point is that medications should be prescribed based on a person's genotype, not their race—which, as we will see in Chapter 13, is a cultural category, not a biological one.

ecological conditions, we contact other species that may carry diseases to which they are immune but that prove deadly to us.

Between 1940 and 2004, a reported 335 infectious diseases emerged, reaching a peak in the 1980s (Jones et al. 2008). The majority of these (around 60 percent) are caused by a nonhuman animal source, and of those, almost 72 percent are from various forms of wildlife. The spike in emergence in the 1980s is possibly a result of increased susceptibility to infection from the HIV/AIDS pandemic.

HIV-1, the virus that is the most common cause of AIDS, crossed over to humans from chimpanzees in West Africa as early as 1931 (Hahn et al. 2000; Korber et al. 2000). (Another virus, HIV-2, came from the sooty mangabey monkey.) Hunting, butchering, and the consumption of undercooked contaminated meat probably accounted for the contact that initially allowed the virus to be transmitted to humans from the nonhuman primates that had evolved the ability to carry the virus with no adverse effects. Early cases were isolated, so the disease didn't spread, even though the virus easily moves from host to host through the exchange

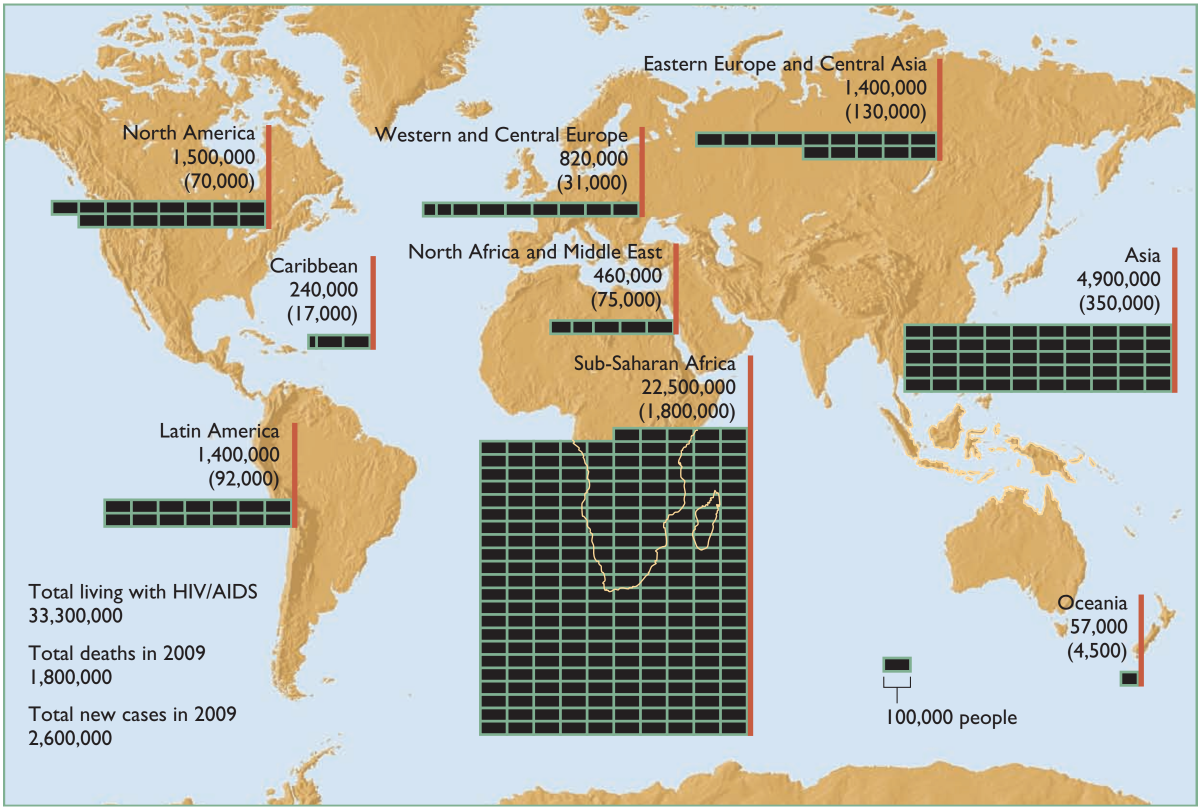

Eastern Europe and Central Asia
1,400,000
(130,000)
North America
1,500,000
(70,000)
Western and Central Europe
820,000
(31,000)
Caribbean
240,000
(17,000)
North Africa and Middle East
460,000
(75,000)
Asia
4,900,000
(350,000)
Sub-Saharan Africa
22,500,000
(1,800,000)
Latin America
1,400,000
(92,000)
Total living with HIV/AIDS
33,300,000
Total deaths in 2009
1,800,000
Total new cases in 2009
2,600,000
Oceania
57,000
(4,500)
100,000 people

FIGURE 12.12
HIV/AIDS in the year 2009. The map shows the number of people, by region, living with HIV/AIDS at the end of 2009. The number of new cases in each region in 2009 is in parentheses. Thirty million people have died of AIDS since 1981. Africa has 12 million AIDS orphans, and worldwide, young people (under 25) account for half of all new infections.
(Source: UNAIDS/WHO 2008)

of bodily fluids during sexual activity or as the result of using unsterilized hypodermic needles. AIDS reached epidemic proportions later in the twentieth century and continues in the present century (Figure 12.12) as a result of social factors, including but not limited to our increased mobility. In addition, the virus itself has evolved since its transmission to humans, producing strains that are drug resistant, more virulent, and hard to detect.

We have long known of another deadly virus—rabies—that is successful because it can jump from species to species (Mills 1997). Hantavirus from rodents, Ebola virus possibly from fruit bats (which is decimating the apes in West Africa; see Chapter 7), and campylobacter, a bacterium from chickens, are some other examples of pathogens that have recently jumped from other species to ours, with serious consequences. Threats from new strains of influenza, such as swine flu and avian flu, seem to appear almost yearly.

Then, there are the *prion* proteins. Prions begin as normal proteins in the nervous tissue of humans, other mammals and birds. These prions, however, sometimes rearrange themselves into abnormal configurations. In this abnormal form, the prions trigger the same rearrangement of the normally configured proteins and then build up in brain tissue, which they eventually destroy. The condition is called *spongiform encephalopathy*. "Mad cow" disease in cattle, Creutzfeldt-Jakob disease in humans, and kuru, a disease described among the Fore people of highland New Guinea, are some examples of this condition, as are other manifestations in sheep, goats, minks, and possibly elk and mule deer. Although the trigger for the abnormal shape of the protein may come, not surprisingly, from a genetic mutation, prions can easily be transmitted across species. Moreover, they are very hard to destroy. Mad cow disease may have spread as the result of cattle being fed meal that contained the remains of other infected domestic animals (Rhodes 1997). Because we now understand the nature and transmission of prions, the incidence of prion diseases has dropped sharply. For a time, though, there were many cases of "mad cow" in Europe (especially Britain), and Creutzfeldt-Jakob is still a threat, affecting, for example, blood donation qualifications.

So, the evolution of our species has been, and is still being, affected by diseases caused by, originating in, and carried by other species that are themselves evolving. An important area for understanding these diseases, then, is evolutionary theory, which explains important factors about their source and transmission. In fact, this approach has been given the name "Darwinian medicine" (Nesse and Williams 1998; Oliwenstein 1995), and I imagine it will become increasingly important in the future.

SUMMARY

While a major focus of bioanthropology is on the evolutionary history of the hominids, the study of the current product of that evolution—modern *Homo sapiens*—is also important. We study living populations of our species from several different yet interrelated approaches.

Since humans live in such a wide range of environmental circumstances, it stands to reason that human groups would have different adaptations to those environments. Most adaptations of our species are cultural, but we still exhibit a number of variable traits based on genetic variations. There is evidence that our variation in these traits is the result of natural selection at some point in our evolution to climatic and other environmental variables.

Among the environmental factors to which humans respond evolutionarily are diseases. Many diseases are caused by or carried by other species, so evolutionary theory may be applied to our understanding of their epidemiology. Viewed from this perspective, we may see some general trends in the relationship between our species and other disease-causing species, in the past and in the present.

QUESTIONS FOR FURTHER THOUGHT

1. The AIDS epidemic (with 30 million deaths so far) could be compared to the Black Death of the fourteenth century (with an estimated 25 million deaths). How do the two epidemics compare? In what ways are they similar or different? Do the effects of the plague of fourteenth-century Europe give us any indication of how the HIV/AIDS epidemic might affect Africa, North America, and Western/Central Europe, where the numbers are on the rise? What sorts of steps should we take to deal with this modern "plague" in this country? in other nations? (To find out what life was like during the Black Death, read chapter 5 of Barbara W. Tuchman's marvelous book, *A Distant Mirror*.)
2. Do you think there is ever a justification for medically treating someone in a particular way based on his or her race? Could race be at least a clue to proper treatment? Or should each individual be treated as the genetically unique person each is? Think about this again after you've read and discussed Chapter 13.

KEY TERMS

melanocytes
melanin

antigens
antibodies

epidemiological

SUGGESTED READINGS

A very useful and well-done book is *Human Biology: An Evolutionary and Biocultural Perspective*, edited by Sara Stinson, Barry Bogin, Rebecca

Huss-Ashmore, and Dennis O'Rourke. It covers in detail many of the topics of this chapter, including adaptation, disease, and population. I highly recommend it.

A nice review article on skin color is "Skin Deep," by Nina Jablonski and George Chaplin, in the October 2002 *Scientific American*. See also "Human Pigmentation Variation: Evolution, Genetic Basis, and Implications for Public Health," by Esteban J. Parra, in the *Yearbook of Physical Anthropology* for 2007 and "Geographic Distribution of Environmental Factors Influencing Human Skin Coloration" in the *American Journal of Physical Anthropology* 125:292–302.

On the topic of the emerging diseases, see Frank Ryan's *Virus X: Tracking the New Killer Plagues out of the Present and into the Future* for a general treatment, Jaap Goudsmit's *Viral Sex: The Nature of AIDS* for a discussion on AIDS, and Richard Rhodes's *Deadly Feasts* for more on prion protein diseases. See "Global Trends in Emerging Infectious Diseases," by Kate E. Jones et al., in the 21 February 2008 *Nature* for some new ideas on that phenomenon. The perspective of Darwinian medicine is described by Lori Oliwenstein in "Dr. Darwin" in the October 1995 issue of *Discover* and by Randolph Nesse and George Williams in "Evolution and the Origins of Disease" in the November 1998 *Scientific American*. See also *Evolutionary Medicine and Health: A New Perspective* by Wenda Trevathan, E. O. Smith, and James McKenna. To keep track of statistics on HIV/AIDS, see www.avert.org/worldstats.htm.

13 CHAPTER

Human Biological Diversity

JEMAAT GKI ZOLNER
Walley

> *Scrutiny of the actual facts shows that*
> *there are only three primary colors*
> *peculiar to the human body; . . . ruddy,*
> *black and brown.*
> *—John Clark Ridpath (1894)*

In the previous chapter we discussed some human variable traits. If our interest in phenotypic variation among modern humans were limited to describing and explaining the distribution of variable traits, we would still have a challenging task. But our biological variation has further meaning to us. Some of our variable traits are distributed with geographic regularity, enough so that one can very often tell from what part of the world a person comes.

People look European or Asian or African or Native American. We can often be more specific: People from Japan don't, on average, look like people from China. Swedes don't look like Italians. Masai from East Africa don't look like the Khoisan from the Kalahari. Inuit don't look like Maya.

Look at Figure 13.1. The photographer in the center and his subjects from the highlands of Western New Guinea are about as different-looking as humans could be, though all are demonstrably members of the same species, *Homo sapiens*. Even if you had not been told where these people were from, and even without the cultural cues of clothing and other artifacts, you could still probably venture a good guess as to their geographic origins. We seem to have evidence, in other words, that our species is divided into a number of fairly distinct subgroups. The term usually applied to such groups is *race*. It seems, on the surface, a logical assumption. Indeed, throughout much of its history, anthropology focused on discovering just how many human races there are and on listing their identifying characteristics.

However, races, on a *biological* level, don't exist within the human species. Races *are* real, but they are *cultural* categories. Every culture responds

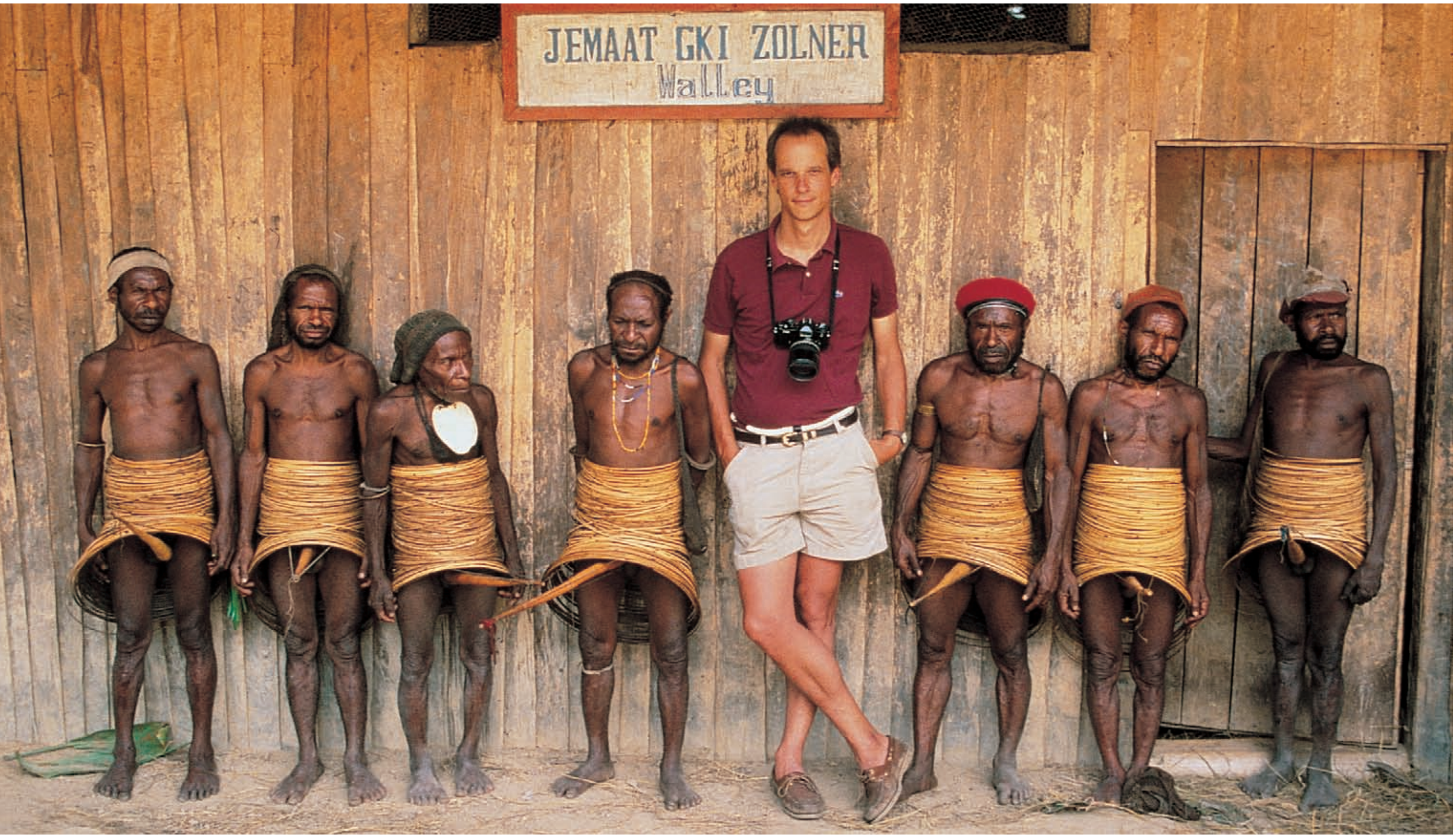


FIGURE 13.1
A European American photographer (6 feet 2 inches tall) stands among a group of Yali men from the highlands of Western New Guinea, or West Papua, part of Indonesia. There is little doubt as to who is who—or that members of our species can display a striking degree of phenotypic variation. The major question then becomes, Does this degree of variation mean that there are distinguishable human races?

to and interprets objective reality—in this case, human biological and cultural diversity—and creates subjective categories that have meaning to its members. A good example of this process, and a somewhat more clear-cut one, is the way in which different cultures translate the biological categories of sex into the cultural categories of gender.

These ideas require more detailed examination, and such an examination is, perhaps, one of the more important contributions of biological anthropology. Let's look at the following questions:

> **How are the two human sexes interpreted differently by different cultures, and how can we use this as a model for examining "racial" variation?**
>
> **Is race a valid biological concept?**

What is the scientific evidence for our statement that there are no biological human races?

What, then, *are* human races?

How can bioanthropology contribute to understanding some of the problems surrounding the idea of race?

SEX AND GENDER

Most human beings are unambiguously either biologically male or female. As noted in Chapter 9, with regard to skeletal features we exhibit sexual dimorphism—varying phenotypic traits that distinguish the two sexes. In living humans, there are still more clearly dimorphic traits.

The biological differences between male and female begin at the genetic level. Two of the human chromosomes are sex chromosomes, X and Y. Females have two X chromosomes; males have an X and a Y. Although the Y chromosome is smaller than the X and carries far fewer genes (several dozen compared with the X's 2,000 to 3,000), it apparently carries a single gene that determines maleness. This gene codes for a protein that triggers the formation of the testes by activating genes on other chromosomes. Products of the testes, including testosterone, then make the developing embryo a male.

Human males, on average, have more body and facial hair and are larger and more heavily muscled than females. They have relatively larger hearts and lungs, a faster recovery time from muscle fatigue, higher blood pressure, and greater oxygen-carrying capacity. Males are more susceptible than females to disease and death at all stages of life. During the first year of life, one-third more males die, mostly from infectious diseases. Males are also more likely to have speech disorders, vision and hearing problems, ulcers, and skin disorders.

Females have a greater proportion of body fat than do males. They mature faster at almost all stages of life, most notably exhibiting earlier puberty and adolescent growth spurt. They are less likely than males to be thrown off their normal growth curve by disease or other factors and, if they are, will recover more quickly than males. Although females appear to have a greater tendency than males to become obese, males suffer more from the effects of obesity—strokes, for example. Females seem to be more sensitive to touch and pain and perhaps to higher sound frequencies, and they are said to be better at locating the sources of sounds. Smell sensitivity is about the same in both sexes, but females seem better at identifying smells. (For more detail, see Barfield 1976.)

Not all of these dimorphic features are understood, and there is a good deal of overlap in the range of variation of these traits—for example, there are some females who are more heavily muscled than some males. But the tendencies do suggest an adaptive explanation. Many of the characteristics of the human male are aimed at sustained, stressful physical action at the expense, however, of overall health. Females' overall better health, earlier maturity, and greater sensitivity to stimulation of the senses might be geared toward their reproductive and child-rearing roles. Perhaps some basic themes of primate dimorphism (we find these size and strength differences in apes as well) were retained and some others selected for in our early ancestors as their small, cooperative bands (described in Chapter 11) confronted the challenges of life in the changing environments of Africa.

Although there is some individual and regional variation in the degree and nature of our sexually dimorphic traits, in general we rarely have any difficulty telling the **sex** of another human being. Male and female are two biological categories that are objectively real and are common to all human groups.

As these two real categories of sex—male and female—are incorporated into various cultural systems, however, differences arise. The identity, place, and role of males and females under different cultural systems vary according to the nature of those systems—their economies, politics, family organizations, and abstract beliefs. Thus, *males* and *females* of the human species become the *men* and *women* of a particular society practicing a particular culture. We refer to the cultural interpretation of biological sex categories as **gender** (Figure 13.2).

From cultural anthropology we acquire data about the incredible range of variation in gender identity and gender roles among the world's cultures. The variable factors include the roles of genders in economic activities, differences in political and other decision-making power and influence, and expected norms of behavior. All these may change over time within a single culture.

For example, in the United States only a century ago, men were educated because they were seen as the gender that properly had political, economic, and social power. Women were far less likely to receive a college education, seldom held any sort of management position (if they did any work outside the home at all), and until 1920 were not allowed to vote in every state. Women were sometimes thought of as "the weaker sex." Obviously things are different now, at least to a degree. As our culture has changed over the past hundred years, our gender roles and identities have changed to fit our evolving cultural system.

sex The biological categories and characteristics of males and females.

gender The cultural categories and characteristics of men and women.

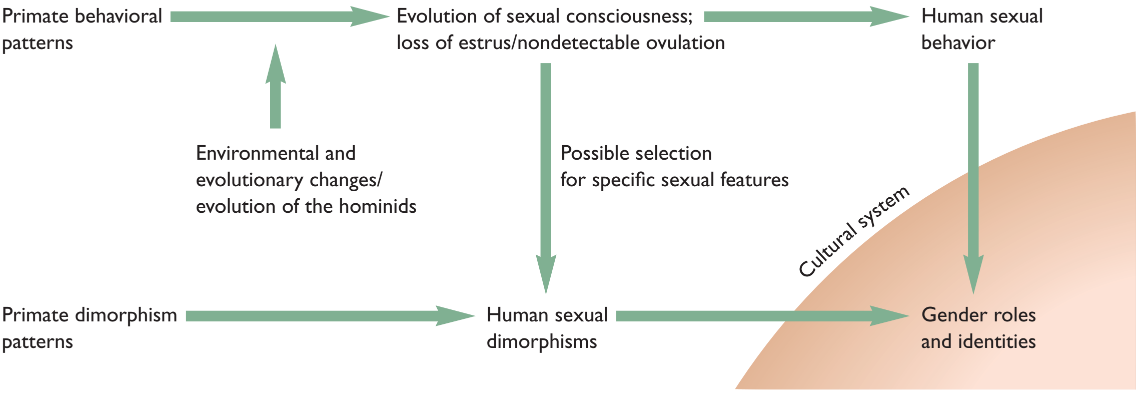

Primate behavioral patterns
Evolution of sexual consciousness; loss of estrus/nondetectable ovulation
Human sexual behavior
Environmental and evolutionary changes/ evolution of the hominids
Possible selection for specific sexual features
Cultural system
Primate dimorphism patterns
Human sexual dimorphisms
Gender roles and identities

FIGURE 13.2
The evolved sexual identities and roles common to all members of the human species are translated by individual cultural systems into gender identities and roles.

We refer to culturally defined categories as **folk taxonomies,** or cultural classifications. Folk taxonomies for gender differ to a great degree among the cultures of the world, even to the point of having more than two gender categories. In part, this is because biological sex is not always unambiguous. There are people born with underdeveloped sexual characteristics, sometimes as a result of having too many or too few of the sex chromosomes. About 1 in every 3,000 female births has a missing or defective X chromosome, and 1 in 500 male births has one or more extra X chromosomes. An estimated 2 percent of humans are *intersexes*, born with characteristics (including genitalia) of both sexes. There is a movement in the United States to recognize such individuals as belonging to categories other than male and female/men and women (Fausto-Sterling 1993, 2000).

Some cultures already recognize more than two genders. Take, for example, the *hijras* of India (Nanda 1990). The word means "not men," and, indeed, hijras are men who have been voluntarily surgically emasculated. They make up a third gender and have very specific identities and roles within the culture of Hindu India. Although often mocked and ridiculed because of their exaggerated feminine expressions and gestures, they are also in demand as performers at important rituals such as marriages and births (Figure 13.3).

Another example comes from a number of traditional Native American cultures in which some men dressed as women and assumed the occupations and behaviors of women. Such men have been referred to by the term *berdache* (a French term with derogatory implications but still in common use). In some cases, they engaged in sexual relations with other

folk taxonomies Cultural classifications of important items and ideas.

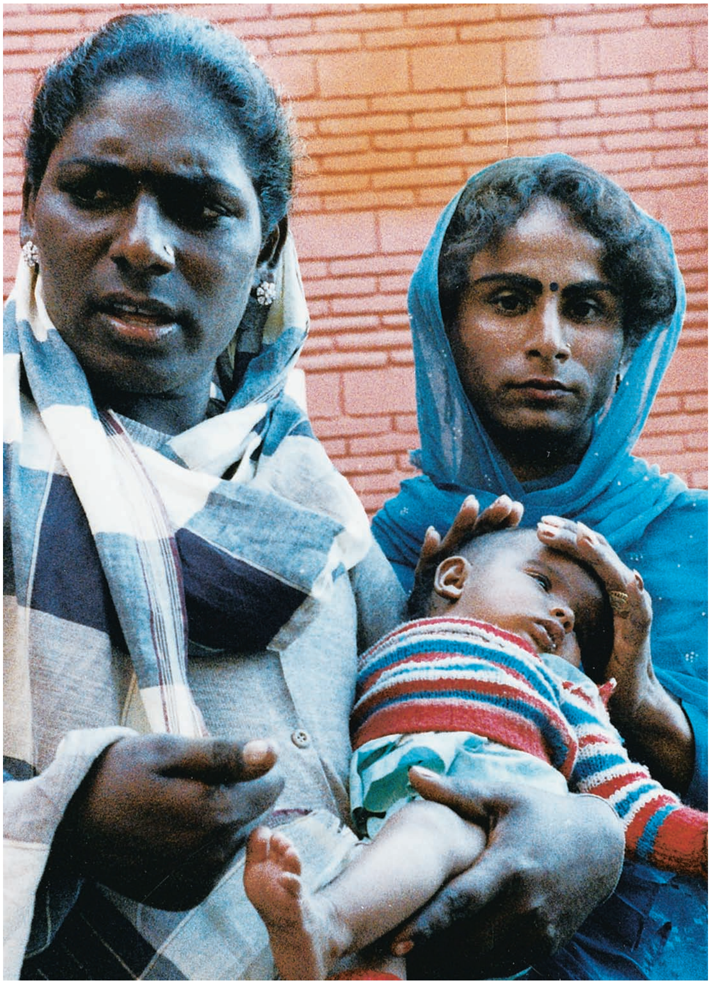


FIGURE 13.3
Hijras, emasculated men who dress and behave like women, make up a third gender category in India. These hijras are blessing a child, one of the important ritual functions they perform.

men, and certain rituals could be performed only by them. Within their respective cultures, berdaches were not considered abnormal but were thought of as a separate gender.

It appears, then, that various societies acknowledge that some of their members are, or think of themselves as, ambiguous with regard to the two standard sex categories. These societies have evolved third or even fourth gender classifications to accommodate them, and these classifications have assumed defined places, identities, and roles within these societies' cultures. Sex is biological. Gender is a folk taxonomy; so, as we will see, is race.

WHY ARE THERE NO BIOLOGICAL RACES WITHIN THE HUMAN SPECIES?

It is all too easy to agree that there are no human biological races because we don't *want* them to exist. The nonexistence of definable racial groups coincides with and reinforces ethical ideas of human equality. But wishful thinking cannot take the place of scientific rigor. We must be able to say *why* there are no races. It's not enough to be sure it's the case or to assume it is because it makes us feel good. We need to present sound scientific evidence for it and realize that it didn't have to be the case; had our evolution been different, distinct biological groups within *Homo sapiens* could have existed.

This evidence comes from four intersecting, interrelated areas. As we discuss them, we need to be as objective as possible, to try not to argue toward a predetermined conclusion. In the end, this will make our affirmation of the nonexistence of biological human races all the more meaningful.

Race as a Biological Concept

The processes of evolution ensure that each species of living thing possesses genetic variation and displays some degree of phenotypic variation. Some species are more variable than others, depending on the nature of the species' geographic distribution and the variety of specific environments to which its members are adapted.

To remain a single species, of course, all males and females of the group must be capable of interbreeding. Furthermore, there must be sufficient gene flow to prevent one or more groups from becoming completely isolated. Gene flow, however, is not always even. Members of a species may be clustered into breeding populations (see Chapter 4). More genes are exchanged within a single breeding population than between different breeding populations, often because some geographic barrier prevents extensive gene flow or because the environments to which the species are adapted come in clusters themselves with gaps between them that limit steady genetic exchange (see Figure 4.5).

Thus, breeding populations may represent phenotypically distinguishable regional populations within the same species. Such breeding populations have been referred to as **subspecies,** or **races.** But all the populations are still members of a single species that maintains its species identity through the flow of genes among those populations. Thus, these subspecies distinctions are artificial. The variable traits grade into one another over geographic space. This

subspecies Physically distinguishable populations within a species.

races In biology, the same as subspecies. In culture, cultural categories to classify and account for human physical diversity.

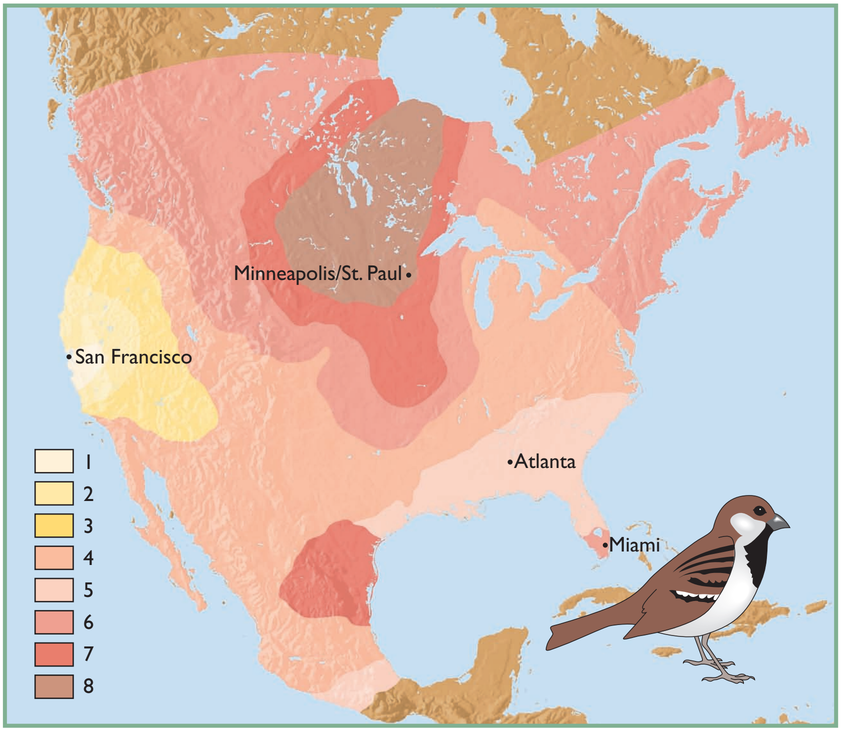


FIGURE 13.4 Distribution of size variation in male house sparrows (determined by sixteen skeletal measurements). The numbers in the key correspond to size: the larger the number, the larger the sparrow. The classes, however, are arbitrary. If a line is drawn from Atlanta to St. Paul or from St. Paul to San Francisco, the size variation in the sparrows is distributed as a cline. (Notice also that the birds tend to be larger in the north, another example of a trait adaptation to the cold; see Chapter 12.)

gradual variation is known as a **cline,** a continuum of change from one area to another, as opposed to a sudden and distinct change (Figure 13.4).

Recent books on evolutionary biology, in fact, indicate that the concept of *race* or *subspecies* is generally falling into disfavor except in special and rare cases. Caribou and reindeer, for example, are able to interbreed but do so only under artificial conditions. In nature, they are isolated in two hemispheres and have been for 10,000 years, developing genetic and phenotypic differences that make them distinct. Thus, they could be considered races or subspecies within their single species.

In Mark Ridley's *Evolution* (2004), for example, neither term appears in the index or glossary, nor is either used formally in the discussions of species variation or formation. In *Population Genetics and Evolution,* by Lawrence Mettler and colleagues (1988), the term *race* is said to be "a subjective convenience." With this background in general biology, then, the question becomes whether humans fit this pattern of a clinal distribution of variation and, thus, cannot be categorized by subspecies or races or whether, as with caribou and reindeer, we come in distinct subspecies.

cline A geographic continuum in the variation of a particular trait.

Human Phenotypic Variation

Given the perceived wide range of human phenotypic variation (see Figures 13.1 and 12.4), could it be that at least some of our populations were isolated long enough to have become distinct enough to warrant subspecies status?

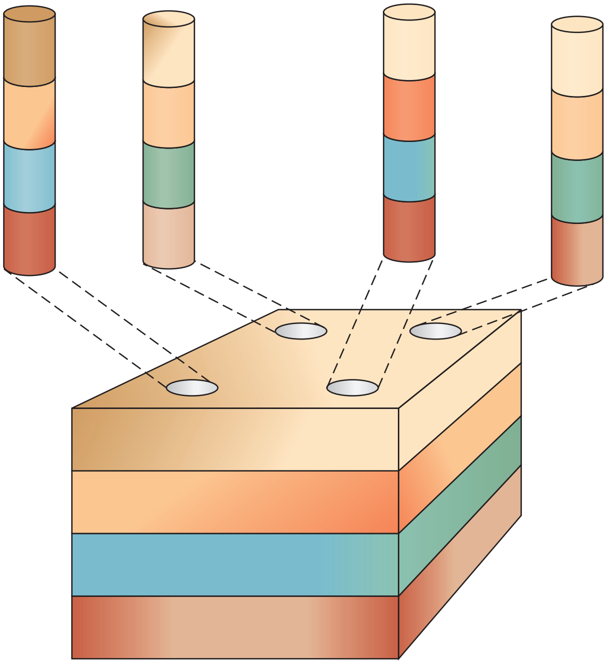
To address this question, we need to go back to Figures 12.7 and 12.8. Although skin color varies by latitude and ranges from very dark to very light, in no way does this variation assort itself into distinct geographic groups. Human skin-color variation, like size variation in the sparrow (see Figure 13.4), is distributed as a cline—gradually going from dark to light or light to dark across geographic space—and is not limited to any one traditional racial population. Dark skin, for example, typically associated with Africa, is an equatorial trait that is also found almost halfway around the world in New Guinea. Clearly, skin color is of no use in defining subgroups within the human species that have any biological meaning.

Skin color, of course, doesn't come in nice, neat categories. It is said to be a continuous trait. So how about traits that do come in discrete, either/or categories? Maybe these would better describe discrete biological populations. Blood type is a good example, since, as discussed in Chapter 12, everyone on earth falls into one of four groups for the ABO system. There are no intermediates.

But look at Figure 12.8. The percentage categories on the maps are arbitrary. I could have divided them into more groups or fewer. Each category is a range and, thus, a generalization. For instance, across Africa, type A is shown to appear in 1 to 20 percent of the population in some areas and 21 to 49 percent of the population in other areas. With more detail, in fact, we would see the distribution of blood-group percentages as clinal, just as we would with skin color. And notice that the distribution of type A is very different from that of type B. In other words, blood-group percentages are of no more use than is skin color in pointing out and defining discrete subspecific human groups.

Nor will such a division show up if we use combinations of traits, because the distributions of traits are discordant—that is, a particular expression of one trait does not necessarily predict a particular expression of another (Figure 13.5). The nature and distribution of human variable traits, then, is like that of most other species—varying as clines with no precise boundaries, despite an often predictable pattern to our biological diversity. Clearly defined biological groups below the species level are not scientifically supported for *Homo sapiens* by the data.

FIGURE 13.5
Diagram of discordant variation. Each layer represents the geographic variation in one variable trait. Each "core," or cylinder, represents a sample of individuals from a particular area. Notice that each core is different and that any other four cores are very likely to be different as well. The expression of one trait does not predict a particular expression of another. There are no natural racial divisions based on specific combinations of traits.
(Based on Ehrlich and Holm 1964:170)



Genetic Variation

Phenotypic features can be deceptive, influenced as they are by multiple genes, environmental factors, and natural selection (see Figure 2.8). For the past several decades, we have had the ability to look at the genetic code itself. Some have thought that perhaps this type of research could provide better data for determining the identity of subspecific groups of *Homo sapiens*.

Earlier genetic evidence clearly indicated that our species was genetically homogeneous, with, for example, about 95 percent of genetic variation between *individuals*, rather than between the large geographic groups often equated with races. Now that we can look at the most basic genetic level, the base pairs of the genetic code, the picture is even more striking.

single nucleotide polymorphism (SNP)
A single base pair of the genetic code that displays variable expressions among individuals.

Of the 3.1 billion base pairs in the human genome, only 10 million show any regular variation at all. Variable base pairs are called **single nucleotide polymorphisms** (or **SNPs**, pronounced *snips*, for short). Because many of these SNPs are rare, the *average* difference between any two individuals on earth is 3 million SNPs. That's less than 0.1 percent variation at that level. And recall that most of the genome is noncoding, so most of those SNPs probably have no phenotypic effect. Moreover, perhaps half of those that do have an effect are involved in the differences between females and males. All the phenotypic variation that we try to assort into race is the result of a handful of genes, the ones that influence traits we *notice*.

What about the differences, though, that do exist, even if few in numbers? Do they show any kind of pattern that would translate into subspecific or racial groups? We can look at combinations of linked SNPs called **haplotypes.** These do, as you would expect, show patterns of variation around the world. (This is not surprising. Phenotypic traits show patterns.) But there are few haplotypes that are *characteristic* of some population or are exclusive to that population. The differences are in frequency of certain haplotypes, such that one might be very common in, say northern Europe, but it would not be *exclusively* found there. Nor would all northern Europeans possess it. The variation is statistical and varies gradually across space. In other words, genetic variation is distributed as clines.

And, finally, when we look at an overall pattern of genetic variation for our species, we find something very interesting indeed. As we noted in Chapter 11 (see Figure 11.44), the genetic variation within sub-Saharan Africa is greater than that for the entire remainder of the human population. Moreover, the variation in the rest of the world is, for the most part, a subset of that of sub-Saharan Africa. Thus, on a broad genetic level, our familiar racial designations don't make sense. "African" is not a genetic race, because there is almost no set of African genetic variation not shared by some other populations in the world. Nor do groups such as "European" or "Native American" have any genetic racial identity because their sets of genetic variants are found somewhere in Africa, the acknowledged geographic "home" of the species.

Thus, as with phenotypic features, variation and regional differences in genes do not translate into support for biologically meaningful racial groups.

Evolutionary Theory

Let's look at the question from a more general perspective. Given the nature of our species and what we know of the workings of evolution, we could ask whether groups distinct enough to be subspecies *could* exist within *Homo sapiens*. We are a populous species; we live in widely varied environmental conditions, sometimes in fairly isolated regions; and we further isolate our populations through cultural boundaries. These would seem to be the perfect circumstances for creating definable races.

However, one noteworthy feature of our species for its entire biological history has been mobility. We evolved first in Africa—whether that was 2 mya or 200,000 ya (see Chapter 11)—and then spread with amazing speed all over the Old World, despite mountains, oceans, and other

haplotype A combination of linked SNPs along a chromosome or stretch of DNA.

barriers. And when we reached the far corners of Africa and Eurasia, we did not stay put. We continued to move around in search of resources and space. As we evolved, we acquired increasing ability to move around (with the domestication of the horse and with inventions such as boats and navigation instruments), and we found increasing motivation for doing so. Such mobility leads to extensive gene flow, and it's fair to say we tend to exchange genes at nearly every opportunity.

But what about our cultural rules of **endogamy?** Don't they genetically isolate populations at certain times? To answer these questions, recall the Hutterites (see Chapter 1), who have been largely endogamous for over 480 years. The Hutterites' nearly half a millennium history is not all that long in evolutionary terms; not much genetic variation can arise over such a short period, especially in a species such as our own with a long generation time. Moreover, cultural rules change, and the political, ethnic, and religious populations they define change over time. Rules of endogamy are not always fully upheld. So, biological isolation through the cultural institution of endogamy is a temporary condition.

Gene flow, then, is the norm for our species, and as widespread as we are, we still manage to exchange enough genes—through intermediary populations—to prevent any group of humans from being isolated long enough to evolve the differences sufficient for subspecies status.

Finally, what about all the different environments our species inhabits? Couldn't natural selection have led to differentiation of some populations? Certainly, the variation and distribution of some of our traits—skin color, for example—can be attributed to natural selection. But our major adaptive mechanism is culture, with its values, social systems, and, especially, its technologies that have increasingly buffered us against the constant editing of natural selection. Adaptively, we evolve culturally. Culture and the big human brain that makes culture possible are species characteristics, shared by all of us. They are the basis of our modern identity. Culture, in a sense, *is* our environment, and we may say that, for some time, our species has experienced little of the kind of environmental variation that would lead to the development of distinct, isolated subpopulations. As anthropologist C. Loring Brace puts it, we all have undergone the "same selective pressures" leading to essentially the "same lifeway" (personal communication).

Thus, aside from what we *want* to think about human biological diversity, sound scientific evidence and reasoning make it clear that there is no basis for the recognition of biologically meaningful groups within the species *Homo sapiens*. Human *variation* exists, to be sure, and some of it shows patterns of geographic distribution. But human *races*—in a biological sense—do not exist.

endogamy Restricting marriage to members of the same culturally defined group.

WHAT, THEN, *ARE* HUMAN RACES?

Like gender categories, human races are folk taxonomies. Several years ago I gave one of my classes a weekend assignment to pose two questions to ten people, preferably from different backgrounds and of different ages and both sexes: How many races are there? What are they?

Nearly all the responses were versions of a familiar set of categories: "white," "black," and "yellow"; or "Caucasian," "Negro," and "Oriental"; or some other terms that varied by individual. The similarity of most responses is an indication that some basic taxonomy is shared among members of our culture.

Societies classify other people relative to themselves. Isolated societies with some knowledge that others exist will have a very simple racial classification: us and them. Among more mobile or cosmopolitan groups, as the relations among people become more varied, the classifications become more complex. These classifications reflect a knowledge about other groups' cultural practices, their relations with our group, and their physical appearance. Thus, a racial taxonomy also carries implications about a society's attitude toward others. In short, race—which differs from society to society—is a folk taxonomy used by a particular society at a particular time for particular culturally based reasons.

The categories of race that we in North America recognize are no exception. The categories' origins can be traced to European knowledge and attitudes first acquired during the Age of Exploration. European explorers, using mostly water transportation, could observe only a limited range of human variation. They sampled points along the clinal continuum of human variation. Because points along a continuum can differ greatly from one another, depending on how far apart they are, it appeared to these explorers that human biological variation fell into a number of relatively discrete categories (Figure 13.6, and see again Figure 13.1).

In addition, the peoples contacted were not seen as simply different human beings; instead, they were compared to and ranked against European peoples, usually unfavorably. They had, after all, a different appearance, different cultures, often less complex technologies, and—important to the Europeans—non–Judeo-Christian beliefs. Furthermore, the motivation for the explorers' voyages was less to acquire knowledge than to find new territories, sources of labor, spices, and precious metals. An attitude of dominance was built into the Europeans' relationships with these new peoples. Witness the way Europeans would claim new lands "in the name of the crown," entirely ignoring the fact that there were already people to whom the lands belonged. Obviously, it was thought, the indigenous people were too primitive to really have laws of ownership.

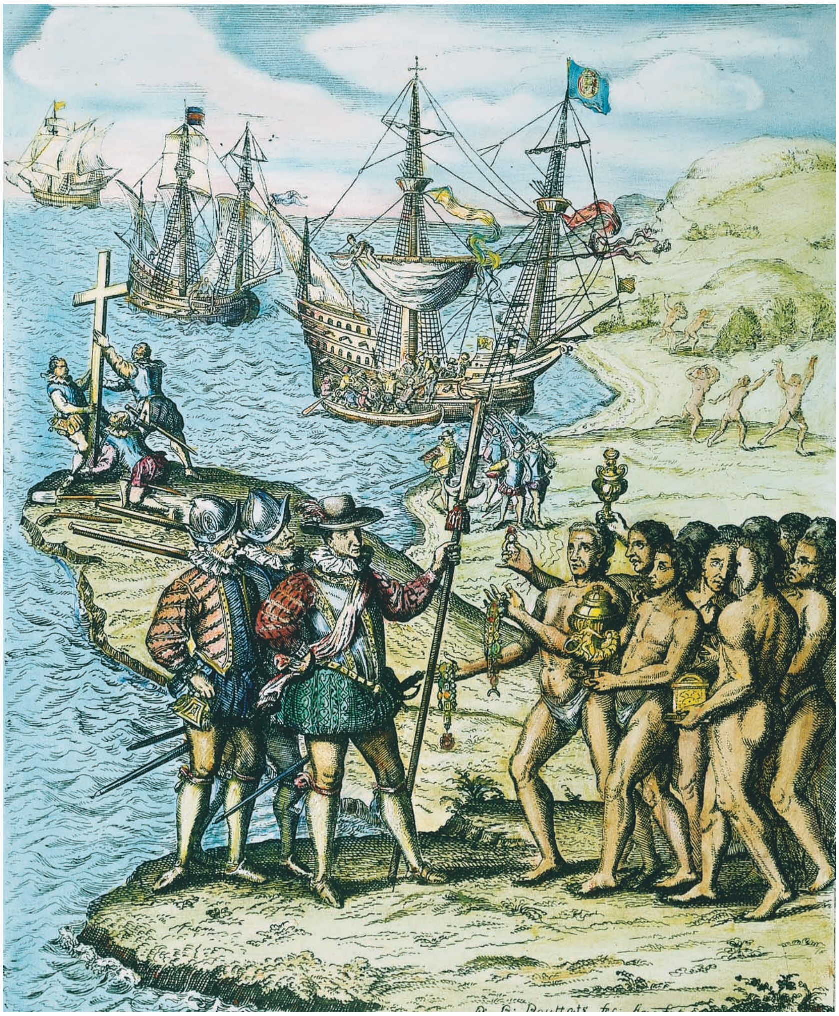


FIGURE 13.6 Columbus's first contact with natives of the New World. To the Europeans, the Indians were so strikingly different physically and culturally that it was natural to consider them as a distinct category of human. Notice the men planting the cross to claim the land as theirs.

(From a seventeenth-century Spanish version of a 1594 engraving by de Bry. The Granger Collection.)

The racial folk taxonomy that resulted from these cultural events was formalized, and thus made more real, by Linnaeus. In the final edition of his taxonomy in 1758, he included *Homo sapiens* and divided the species into "varieties," or races. Actually, he recognized a second species, *Homo monstrosus*, to accommodate explorers' yarns of wild "half-men" covered with hair and sporting tails, and he recognized a variety of *Homo sapiens* he called *ferus* ("wild man") for the probably retarded and abandoned children who were sometimes found wandering in the woods and were said to have been raised by wolves and other animals. His main races were American, European, Asiatic, and African, and his descriptions of these races were a blend of biological generalizations and, as Stephen Molnar says, “personality profiles” based on European perspectives (1992:10). Here is Linnaeus’s taxonomy for humans (based on translations in Gould 1996b and Kennedy 1976):

Class: Mammalia
  Order: Primates
    Genus: *Homo*

Species: *monstrosus*	Varying by climate or art
sapiens	Diurnal; varying by education and situation
Varieties:	
ferus	Four-footed, mute, hairy
americanus	Red, choleric [angry], upright. Hair black, straight, thick; nostrils wide; face harsh; beard scanty; obstinate, content free. Paints himself with fine red lines. Ruled by habit.
europeaus	White, sanguine [cheerful], muscular. Hair yellow, brown flowing; eyes blue; gentle, acute, inventive. Covered with cloth vestments. Ruled by custom [or law].
asiaticus	Pale-yellow, melancholy, stiff. Hair black; eyes dark; severe, haughty, covetous. Covered with loose garments. Ruled by belief [or opinions].
afer	Black, phlegmatic [sluggish], relaxed. Hair black, frizzled; skin silky; nose flat; lips tumid [swollen]; crafty, indolent, negligent. Anoints himself with grease. Ruled by caprice [impulse].

Sound familiar?

Because the history of the United States has been so influenced by European cultures, it makes sense that these basic categories and attitudes would be carried over to this country and altered by its subsequent history. For example, the reason we distinguish Hispanics from other European Americans is, in part, because of the conflicts between Spain and other European countries over territory in the New World and later between Mexico, a former Spanish colony, and the United States. Notice, too, that in some lists of race, Puerto Rican has been separated from Hispanic. It’s not that some new group of people has arisen but rather that, for census purposes, we choose to distinguish people from that U.S. territory—people who previously and still in other lists are categorized as Hispanic.

Our racial categories are real. They may not reflect universal biological reality on the species level, but they do have meaning within our cultural system, for better or for worse.

ANTHROPOLOGY AND THE HISTORY OF RACE STUDIES

It would be nice to say that anthropology has all along been the discipline that debunked the concept of biological race and collected real data to support the nonexistence of races. But this is not the case. As we discussed in Chapter 1, anthropology is a science conducted, as are all sciences, within a cultural context and so is influenced, even constrained by, cultural trends and limits of possible knowledge. The fact is, for much of the history of anthropology, into the 1960s, the field acknowledged some racial divisions of humankind and sought to enumerate and define those races.

Going back into the nineteenth century and earlier—before anthropology even was a named field—there was, of course, scientific interest in explaining human biological and cultural variation, and the reality of biological races seemed as obvious as the reality of different cultural systems. Often, both these areas of variation were explained as different stages in the evolution from a more primitive to a more civilized state, with the obvious value judgments that implies.

In the early twentieth century, Franz Boas (often called the "father of American anthropology") challenged the validity of "types" of humans and said that differences in achievement among cultures were the results of historical events, not of differences in mental faculties. Still, the reality of races was, more often than not, assumed. Museum displays well into the middle of the century included family trees with branches to the typical races, and popular and scholarly books divided humankind into a usually small number of relatively distinct groups.

The virulent and violent racism of Nazi Germany in the Second World War led to a rethinking of the accepted reality of race that, if not the cause of such racism, certainly helped facilitate it. As early as 1942, anthropologist Ashley Montagu wrote *Mans' Most Dangerous Myth: The Fallacy of Race* and in 1964 he edited *The Concept of Race*, a collection of eleven essays that debunk the concept using the same reasoning—if not all the modern data—of the argument in this chapter.

Still, the idea that races must exist lingered and still does. My first course in human variation, in 1967, was titled "Varieties of Man," the name implying that there *were* varieties. My class notes included lists of characteristics of the major races, with other lists for "hybrid" races. And the text was *The*

Origin of Races by University of Pennsylvania anthropologist Carleton S. Coon. The book not only recognized five original races but claimed that those races could be traced back, through fossils, to *Homo erectus* and had crossed a "sapiens threshold" at different times and in a particular order. The races, thus, had been "sapient" (it means *wise* or *intelligent*) for different lengths of time. This explained, claimed Coon, the differences in cultural complexity and achievement around the world. (It's almost unnecessary to relate in which order Coon thought the races had crossed this imaginary threshold.)

And even as recently as 2004, anthropologist Vincent Sarich and science writer Frank Miele claimed in *Race: The Reality of Human Differences* that "race is a valid biological concept" in part simply because we recognize races in common cultural discourse. In making this argument, they ignore the difference between biological reality and folk taxonomy that we've discussed. Old folk taxonomies sometimes die hard.

It must be made clear again that the claim that biological human races don't exist is not being made because it would bolster moral and ethical precepts of human social equality. That is a separate issue. The fact is, based on sound scientific reasoning, human biological races don't exist—whether we like that or not. And this has been, despite aspects of its past history, a major contribution to knowledge that anthropology can take almost full credit for.

RACE, BIOANTHROPOLOGY, AND SOCIAL ISSUES

The issue of race in the human species is not just a matter of whether to apply the biological concept of subspecies. If only it were. Rather, the idea of race can be, and is, used to make prejudgments about people and to determine their place in society, often without regard for their individual characteristics. This is **racism.** The moral dimension of this problem should be important to everyone, but it is not something we can or should deal with in a brief book about bioanthropology. We may, however, show how bioanthropology, through the use of science, can examine some claimed connections between racial categories and biological traits. In so doing, we can inform ourselves more fully about just what race is and what it is not. Let's briefly look at two topics.

Race and Intelligence

If a group of people were interested in limiting the social position and power of another group, they could argue that the other group possessed some unalterable biological difference that inherently limited their abilities and therefore justified their lower social status. The practice of slavery

racism Judging an individual based solely on his or her racial affiliation.

in the United States was often justified by the claim that the African slaves were biologically less intelligent than the whites and therefore could never hope to attain the dominant race's social, political, and intellectual level.

Such broad statements about race and intelligence, or even race and evolutionary level, are so clearly motivated by social and economic aims as to be at least questionable, if not obviously false. Perhaps more dangerous, however, are correlations whose propositions seem scientific.

Such is the case for the claimed connection between race and IQ (intelligence quotient). The most famous (or infamous) example is educational psychologist Arthur Jensen's 1969 article in the *Harvard Educational Review* titled "How Much Can We Boost IQ and Scholastic Achievement?" A more recent work, *The Bell Curve* by Richard Herrnstein and Charles Murray (1994), repeats and greatly expands the same essential argument (see Gould 1996b for a detailed critique).

A focus of Jensen's article was the documented fact that American black children score, on average, fifteen points lower on IQ tests than American white children. Jensen wondered why programs aimed at culturally enriching children's lives had basically failed to eliminate the fifteen-point IQ difference. Hence, the title of his article (emphasis mine for the right intonation): "How Much CAN We Boost IQ and Scholastic Achievement?"

Jensen concurred with earlier researchers that IQ tests measure an entity called *g*, or general intelligence, and that the differences between groups in general intelligence are largely biological and genetically inherited, with only limited influence from one's environment. Obviously, then all the cultural enrichment programs in the world can have only minor effects. In response to his own question—How much can we boost IQ and scholastic achievement?—Jensen concluded, Not much. He stated, "No one has yet produced any evidence based on a properly controlled study to show that representative samples of Negro and white children can be equalized in intellectual ability through statistical control of environment and education" (1969:82–83).

Jensen's article caused a great deal of controversy. He was labeled a racist, and those with racist leanings embraced his work enthusiastically. Let's look at his article from a scientific point of view, drawing especially on what we have learned from anthropology.

The idea that IQ tests measure some innate mental ability is fraught with problems. It has been said that IQ tests measure the ability to take IQ tests. This is not just a sarcastic remark. Intelligence is a complex phenomenon. How, then, can we apply a single number to such a concept through a test given in a cultural language, in a cultural setting, with cultural problems? When we do this, we commit the logical error called **reification.** With IQ scores we have reified intelligence—translated a complex idea

reification Translating a complex set of phenomena into a single entity such as a number.

into a single entity, in this case a number, which we then use to divide people into groups such as different learning tracks in schools.

Let's put this another way. As anthropologist Jonathan Marks suggests, there is a difference between *ability* and *performance* (1995:240 ff.). One's score on an IQ test is a score of one's performance. Certainly some internal factor—innate intellectual abilities, whatever those are—plays a part in one's performance on an IQ test. But that performance is also affected by external factors such as your cultural background, quality of education, personality, home life, even your mood on the day of the test. We cannot, therefore, infer innate abilities from the test score, any more than we can, say, infer a person's athletic abilities from his or her performance in one game. We have no way of accounting for external influences, controlling them, or even knowing what they are. Thus, "IQ measures not just the quality of a person's mind but the quality of the world that person lives in" (Gladwell 2007:96).

Finally, if you are looking to make biological comparisons between two groups, the groups need to be biologically defined. American whites and American blacks are decidedly not biological groups. We perceive differences between American blacks and whites-average skin color, major geographic area of origin, frequency of diseases such as hypertension, and even frequency of some genes such as that for sickle-cell anemia—but the groups themselves are cultural. Indeed, it has been estimated that about 15 percent of African Americans' genes are of European American origin as a result of gene flow between the two populations over the past several hundred years (Lewontin 1982).

So, the difference in performance on IQ tests can be seen as heavily influenced by the socioeconomic limitations imposed on African Americans over the past several centuries, limitations that have resulted in separate and often poor-quality education, limited access to various forms of cultural enrichment, and even the psychological effects of being identified as members of a minority group. These are all intangible factors that are impossible to fully control or even identify. And we certainly cannot make a biological generalization about a whole culturally defined group of people based on those performance results.

Race and Athletic Ability

Nearly 80 percent of players in the National Basketball Association are African American. The figure is 70 percent for professional women's basketball. The National Football League is 65 percent black. In long-distance running, nearly every men's world record belongs to an African or someone of African descent. In the 2011 New York Marathon, three of the top ten male finishers were from Kenya, including the first and second finishers; numbers three and four were Ethiopian. The top female finisher was Ethiopian and three of the top ten were Kenyan. In the 2011 Boston Marathon, five of the top ten men were Kenyan, including numbers one and two, and four were Ethiopian. Kenyans came in first, third, and fourth for the women. These statistics pose an obvious question, which we may address by focusing on a controversial book by journalist and TV producer Jon Entine called *Taboo: Why Black Athletes Dominate Sports and Why We're Afraid to Talk About It* (2000). Entine wrote it, he says, because "sport remains a haven for some of our most virulent stereotypes" and because he believes "that open debate beats backroom scuttlebutt" (8). And open debate it does.

Our immediate explanation for the disproportionate representation of athletes of African descent in some sports is what might be called "social selection." This is the idea that in this country and others, sports—particularly those not requiring specialized and often expensive equipment—became an outlet for members of minority groups, an achievable goal when access to opportunities such as higher education and careers were limited by social prejudices, poor primary and secondary education, and lower socioeconomic status.

Entine points out that this, in fact, was the case with Jews and basketball in the first half of the twentieth century; basketball (as well as boxing) was a way out of the ghetto and ethnic prejudice. So stereotyped did the association between Jews and basketball become that one 1930s sportswriter made a semibiological connection, claiming that Jews were better at the game because of their "alert, scheming mind" and "flashy trickiness" (quoted in Entine 2000:203).

But Entine also claims that there are biological explanations and that these are, in some cases, more influential. Specifically, he documents evidence that three regions of Africa—the west coast, North Africa, and East Africa—have populations with physical attributes more common to them than to other populations that make them innately better at sports involving endurance, sprinting, and jumping. These traits include such things as a lower percentage of body fat, a higher proportion of certain muscle fibers, and physiological features related to the efficiency of oxygen use. He says that the reason these traits—of obvious adaptive utility—are more common in Africa is that "while people of African descent have spent most of their evolutionary history near to where they originated, the rest of the world's populations have had to modify their African adaptations after migrating to far different regions and climates" (18).

The arguments in Entine's book and in reviews of it (Bogin 2001; DiPietro 2000; Malik 2000, for example) are complex and require further discussion and examination, but for our purposes here we can address two issues. First, is it possible that there are variable human phenotypic traits, even ones showing patterns of geographic distribution, that might relate to athletic ability? Of course it is. How many heavyweight boxers could hail from the highlands of Western New Guinea (see Figure 13.1). Could the average Inuit compete successfully in a 400-meter sprint against someone built like the Masai in Figure 12.4?

And why couldn't physiological differences that have an impact on athleticism exist? Some performance-enhancing drugs are versions of natural human biological products; anabolic steroids, for example, are synthesized versions of testosterone. Recent experiments have used gene therapy on mice and rats to increase levels of IGF-1, a protein that promotes muscle growth and repair, resulting in bigger, stronger rodents (Sokolove 2004). In theory, genetic variation in humans, some of which could show a geographic pattern, might lead to such phenotypic variation. Moreover, social factors, motivation, and practice can explain only so much. As sportswriter Michael Sokolove puts it (2004:32), "You cannot will yourself into an elite athlete, or get there through punishing workouts, without starting out way ahead of the rest of the human race."

But the problem with Entine's overall argument is that he uses individuals who are exceptional (for whatever reason) to make generalizations not only about particular populations (such as the Kenyan runners) but about whole "racial" groups as well. He starts with the assumption that these groups exist and have some degree of time depth, definition, and internal homogeneity. He says, for example, that "although there is considerable disagreement, the *three major racial groupings—Caucasian, Mongoloid, Negroid*—split from 100,000 years ago to as recently as the beginning of the last ice age" (113; emphasis mine); he even espouses a minority view that "different races [may not be] modifications of *Homo sapiens*, they were in existence before the emergence of *Homo sapiens*" (116). (Recall Carleton Coon's model described in the last section.) In other words, he assumes that the populations he is examining *are* races in the traditional, biological sense of that word. This, then, is the basis for his explanation of the dominance of African Americans in some sports, namely as a result of their African heritage. According to Entine, Africans are, on average, innately better athletes for some skills, and so a great number of African Americans have inherited these innate skills.

These are logical leaps with little if any validity. We understand that variation exists and that some is geographically patterned. But clear-cut racial groups do not exist. While a small Kenyan population just might have some features that make them better runners (and the more common idea is that they simply practice a lot and under the right conditions!), that in no

Contemporary Reflections

Are Genetic Ancestry Tests Worth the Money?

A couple dozen companies in the United States now offer so-called genetic ancestry tests. These services purport to help people determine their geographic area of origin, their "homeland" if you will. Probably a million people so far have paid anywhere from $100 to $900 for this service (Bolnick et al. 2007). At least one company specifically focuses on African Americans, to help them connect to existing African groups and at least begin to recover information about their lost heritage as a result of the slave trade (Lehrman 2006).

How do these tests work? Most genetic-testing services use sections of a client's mtDNA or Y-chromosome DNA. (Mitochondria (see Figure 3.1) are the cells' energy factories and have their own DNA, called mtDNA. You inherit mtDNA only from your mother. Y-chromosome DNA is only inherited from your father.) A few use sections of nuclear DNA. They then look for locations where the client's haplotypes (collections of genetic variables) are found. As we discussed, there are patterns that can be found in human genetic diversity (Li et al. 2008). This is no surprise. There are patterns of phenotypic diversity as well. But the nature of the genome and of the distribution of genetic diversity severely limits the accuracy and usefulness of these ancestry analyses.

First, with mtDNA or Y-chromosome DNA, only 1 percent of a person's genome is being tested, and only one lineage is being traced back through time—your mother's or your father's. This leaves out a lot of people! It would be as if I tried to reconstruct my family tree by tracing my family only from my father, through my grandfather, great-grandfather, and so on. I followed such a path, going back from father to

way means that those features are necessarily more common on the African continent, because this assumes that Africa is synonymous with a racial group. And it certainly doesn't explain the sports phenomenon in the United States. Among other problems with Entine's conclusions is the fact that the average African American can trace a fair percentage of his or her genes to Europe. This should mean that African Americans would be worse athletes than specific populations of Africans, but this is not the case (Malik 2000).

This is a complex issue. Obviously, *both* biological and sociocultural components contribute in different degrees to various aspects of sports. We should not be afraid to examine this issue. But doing so in terms of demonstrably nonexistent biological races only serves to detract from an accurate understanding of the topic and might further reinforce those "virulent stereotypes" that Entine justly seeks to refute.

Our folk taxonomies are powerful and influential. We respond to them often without realizing that they are *our* culture's way of ordering *our* world and are not necessarily scientific universals. The influence of the American folk taxonomy for race can easily be seen in Jensen's and Entine's work. By understanding what race is—and what it's not—and by applying what we know about the workings of genetics and evolution, we may see the fallacies father to one John Parke, born in England in 1530. It was very interesting. But as I worked my way back, with each generation I accumulated an increasing number of ancestors. John Parke lived thirteen generations ago. At that time I had 8,192 (2^{13}) ancestors. And I know about only one of them. I don't know about the other 8,191. A lot of my biological heritage, and probably a lot of geographic locations, never showed up.

Second, most haplotypes are not exclusive to specific groups and are thus not diagnostic of those groups. The differences between groups are matters of relative percentage. Moreover, the databases used by the services are limited to a sample of living groups from various regions and then a sample of people within those groups. So while it is likely, for example, that many of my haplotypes would match those of samples from northern Europe or the British Isles (no surprise there), other geographic areas of my heritage could be entirely left out. Or, I could have some haplotype that is very frequent in a regional population that has no recent or direct connection to my heritage and thus would produce a false result.

Third, clients are often searching for—and these services tell them—what racial or ethnic group they are part of. (Oprah Winfrey was told by one such service that her heritage was Zulu.) The problem is, as we have seen, that there is no clear-cut connection between genetics and racial or ethnic affiliation. Culturally defined groups change over time in location, composition, and boundaries. (Zulu is a linguistic and cultural group, with a complex history, not a biological group.)

So, are genetic ancestry tests worth the money? The answer is no—if what you're interested in determining is your biological heritage or your ethnic or racial membership. As Bolnik et al. (2007:399) put it, these ancestry services are examples of "recreational genetics."

of these and similar studies. This perspective is an important one for helping us deal with the other issues of race that confront us almost daily.

SUMMARY

Human societies need to find order in and make sense of the environments in which they live. Cultural systems, therefore, translate objective reality into categories that have meaning to them. We call these categories folk taxonomies.

So important are the relationships between the sexes and the relative places in society of males and females that different cultural systems have evolved very different folk taxonomies for sex. These are gender roles and identities, and in some societies they may even comprise more than two genders if those societies formally classify persons of ambiguous sex or sexuality.

That humans in general display variable traits is obvious, on some level, to all societies. Thus, all cultural systems include folk taxonomies for race. On a biological level, however, races (or subspecies) do not exist for our species. Indeed, the concept of race is falling from use in biology in general. But even if we attempt to apply the race concept to humans, we find that the biological nature of our species does not lend itself to division into clear-cut, discrete units.

So powerful is the folk taxonomy for race that our categories take on a reality beyond that which is warranted, and we find that we use them as cues to tell us how to think about other groups of people and how to treat them. We can all too easily confuse culture and biology, and this effect can even be seen in scientific investigations, such as those that look for some biological racial difference in the cultural measure of intelligence called IQ or in athleticism.

QUESTIONS FOR FURTHER THOUGHT

1. Expand upon the brief discussion in the text concerning the identities and roles of the two genders in North American culture. How would you characterize them? How have they changed during your lifetime? Do you see a need for further change? Why? How could such change be achieved?
2. Still looking at your own culture, think about gender categories. Are there just two? Should there be more in light of what we know about the frequency of intersexes? Are more categories possible within this culture? Where does homosexuality fit into this discussion?
3. Discuss further the North American categories of race. What specific historical events or sequences may have influenced our commonly understood racial groups? If you are familiar with the racial taxonomy of another culture, similarly analyze it.
4. Apply the race and athleticism argument to a specific stereotype: "White men can't jump." Watching an NBA game, it sure appears to be true. Explain why it seems that way. What *is* true about the stereotype?
5. On a practical level: Suppose it was shown that some populations in Kenya have a disproportionate number of members who possess physical and physiological features that make them better runners. How should we accommodate this in organized sporting competitions such as the Olympics to level the playing field?

KEY TERMS

sex
gender
folk taxonomies
subspecies
races
cline
single nucleotide polymorphism (SNP)
haplotype
endogamy
racism
reification

SUGGESTED READINGS

A good book on sex and gender from an anthropological perspective is *Female of the Species*, by M. Kay Martin and Barbara Voorhies. Despite the title, it is really about both sexes and all the gender categories found in various cultural systems. The fascinating case of India's hijras is documented in *Neither Man Nor Woman: The Hijras of India,* by Serena Nanda. I cover the topic of sex and gender in more detail, with more on the cultural dimension, in my *Introducing Anthropology: An Integrated Approach*.

On race, I highly recommend *Human Biological Variation*, by James Mielke, Lyle Konigsberg, and John Relethford; *"Race" Is a Four-Letter Word,* by C. Loring Brace; and the classic but still current *Man's Most Dangerous Myth: The Fallacy of Race*, by Ashley Montagu.

For a collection of articles on the nonexistence of human biological races, see *The Concept of Race*, edited by Ashley Montagu, and for a nice treatment of the history of race studies, try Kenneth A. R. Kennedy's *Human Variation in Space and Time*. Also, see the chapters on race in Jonathan Marks's *What It Means to Be 98% Chimpanzee*, *Why I Am Not a Scientist*, *and The Alternative Introduction to Biological Anthropology*.

The best book on racism, emphasizing an examination of scientific attempts to find correlations between race (and sex) and intelligence, is Stephen Jay Gould's *The Mismeasure of Man*.

I do recommend Jon Entine's *Taboo*. Even though I disagree with major aspects of his analysis, his thought-provoking book succeeds very well in its goal of stimulating open debate on the subject.

An interesting piece on IQ is "None of the Above," by Malcolm Gladwell, in the 17 December 2007 *New Yorker*.

For more on ancestry testing, see "The Science and Business of Genetic Ancestry Testing," by Deborah A. Bolnick et al., in the 19 October 2007 issue of *Science*, and two letters in response in the 22 February 2008 issue of *Science* beginning on page 1039.

If you want to trace some of your own family's genealogy, try www.rootsweb.ancestry.com.

14 CHAPTER

Biological Anthropology and Today's World

We too are part of history's seamless web.
—Reinhold Niebuhr

On September 11, 2001, Amy Zelson Mundorff, a forensic anthropologist, was at her job at the New York City medical examiner's office. When news broke of the attacks on the World Trade Center, she and three coworkers rushed to the site to lend their aid. Shortly after they arrived, the South Tower collapsed and Mundorff narrowly escaped with her life. She nursed her injuries for two days before returning to her job as one of the first to examine the more than 16,000 human remains from Ground Zero. In 2002 she was among those cited by New York City Mayor Michael Bloomberg for her courage on that day and her leadership afterward in identifying some of the victims.

Although certainly not to everyone's taste, such work is one of the ways that biological anthropology makes a tangible contribution to our lives. It is, of course, unfortunate that such services are needed. But they are, and the work of identifying human remains and, sometimes, of identifying the cause of death is an important one, bringing some comfort to the survivors and perhaps justice to the slain.

Although the work of all biological anthropologists is useful in its contribution to knowledge, there are some practical ways in which our field can be applied and some lessons all people can learn from biological anthropologists' unique perspective on our species. In this last chapter, we will address the simple question:

What are some of the applications and lessons of biological anthropology?

FORENSIC ANTHROPOLOGY: READING THE BONES

One meaning of the term *forensics* is "the application of science to legal matters." The skills anthropologists use to retrieve information from ancient skeletons (see Chapter 9) have also proved useful in retrieving information from more modern ones—the victims of violent crimes and accidents. In turn, some of the methods developed by forensic anthropologists have been applied to older remains that are of scientific, rather than legal, interest.

Perhaps the best-known case of the latter is the well-publicized "Ice Man," or "Ötzi." He was found by hikers in September 1991, at over 10,000 feet in the Ötztaler Alps, on the Italian side of the border with Austria. He had been naturally mummified by the dehydrating action of the cold and the wind and was in a remarkable state of preservation. The find became all the more remarkable when carbon-14 dating of the body itself, and of grass with which he had stuffed his boots, provided a date of 3300 BC. The body was over 5,000 years old.

The Ice Man was found with a fascinating array of artifacts, including much of his clothing and some tools. Details on these may be found in the readings listed at the end of the chapter. Here, we'll concentrate on the body itself (Figure 14.1).

Investigators X-rayed the body and, using techniques we discussed in Chapter 9, determined that it was that of a male about 5 feet 2 inches tall. He was around 46 when he died. Oddly, he has only eleven pairs of ribs, instead of the usual twelve, and his seventh and eighth left ribs had been broken at one time or another but were healed at the time of his death. There is some evidence of hardening of the arteries, and his lungs were blackened, probably by smoke from open fires.

There are sets of parallel lines on the Ice Man's lower back, left thigh, and right ankle that are charcoal-dust tattoos. An early hypothesis is that these tattoos, near Chinese acupuncture points, were therapeutic measures to relieve arthritis (Stone 2000), but recent X-rays have revealed little or no evidence of that condition (Dickson et al. 2003).

The Ice Man's teeth show considerable wear, some of which can be clearly seen on his upper incisors. This probably indicates that he used his teeth as tools, perhaps for leatherworking, and that he ate a tough diet including dried meat and the products of flour from grains that had been mixed with sand to aid in grinding. Both practices are known from the archaeological record.

His diet, however, may not have been particularly good. Patterns on a fingernail recovered later (the others had fallen off) suggest periods of

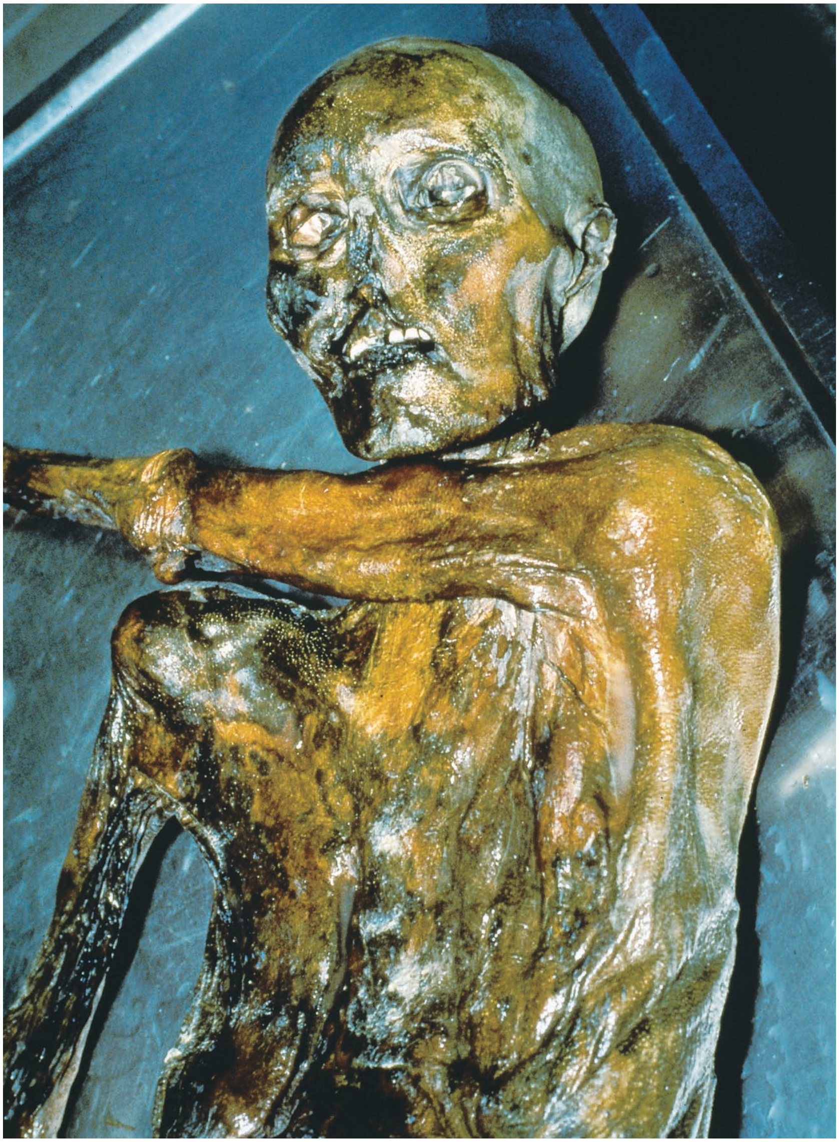
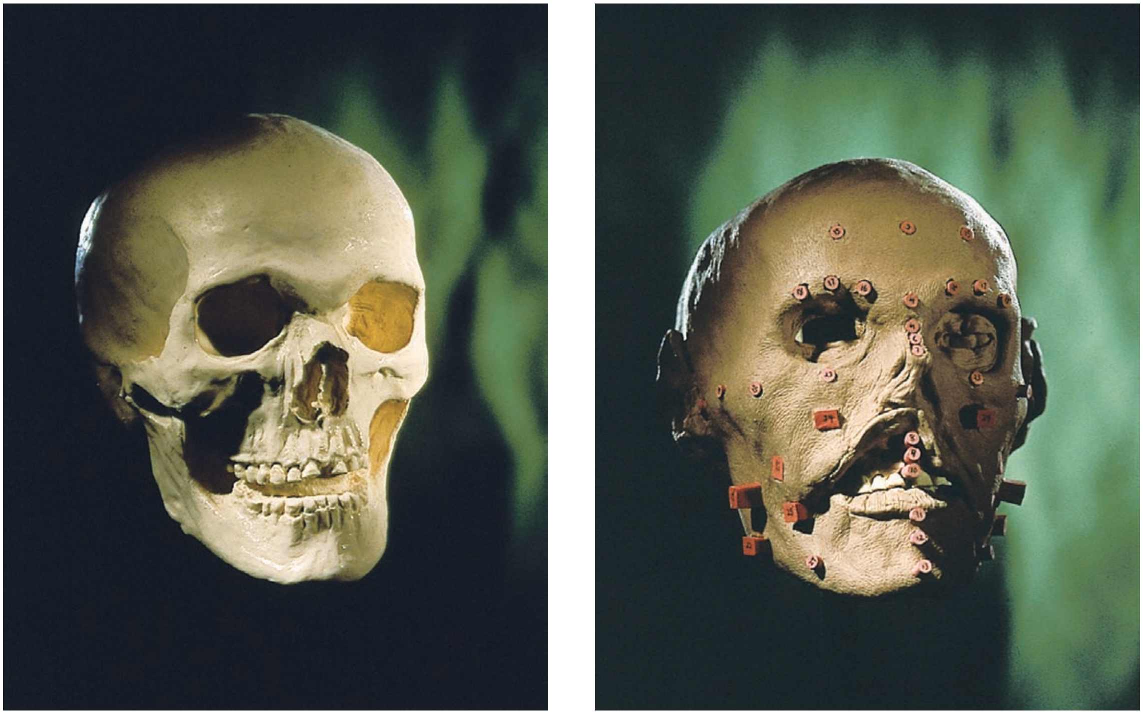


FIGURE 14.1
The Ice Man's body, preserved for over 5,000 years in the Italian Alps, was naturally mummified by cold and wind. Pressure from the ice disfigured his nose and lip and pushed his left arm into this odd position. We are still learning about his life and death from his preserved body, which includes his brain and internal organs.

reduced nail growth from disease or malnutrition. And eggs found in his stomach show that the Ice Man suffered from an intestinal parasite called a whipworm. The parasite causes diarrhea and acute stomach pains.

When and how did Ötzi die? For years, the assumption was that he had died of exposure, caught in rapidly deteriorating conditions in the



mountains in early fall. But more recent studies of food residue in his colon revealed pollen from a tree that flowers in late spring and early summer. And in 2001, an X-ray showed an arrowhead embedded in his left shoulder that might have been the cause of his death. Moreover, his right hand shows a deep stab wound, and DNA analysis suggests that his clothing and tools had the blood of four other persons on them (*Science* 2003). The plot thickens.

Finally, in part to put to rest the inevitable questions about possible fraud, scientists performed DNA analysis. It indicated that the Ice Man was a European and that he was related to living populations from the northern Alps (keep in mind the limitations of such techniques discussed in the previous chapter). Techniques of reconstruction have even given us an idea of what he looked like (Figure 14.2). And some new research (Müller et al. 2003) using isotope comparisons of soil and water samples with samples from Ötzi's teeth and bones, and argon/argon dating of mica pieces in his intestine, has even pinpointed where he lived—a valley about 60 kilometers south of where his body was discovered. In fact, a new

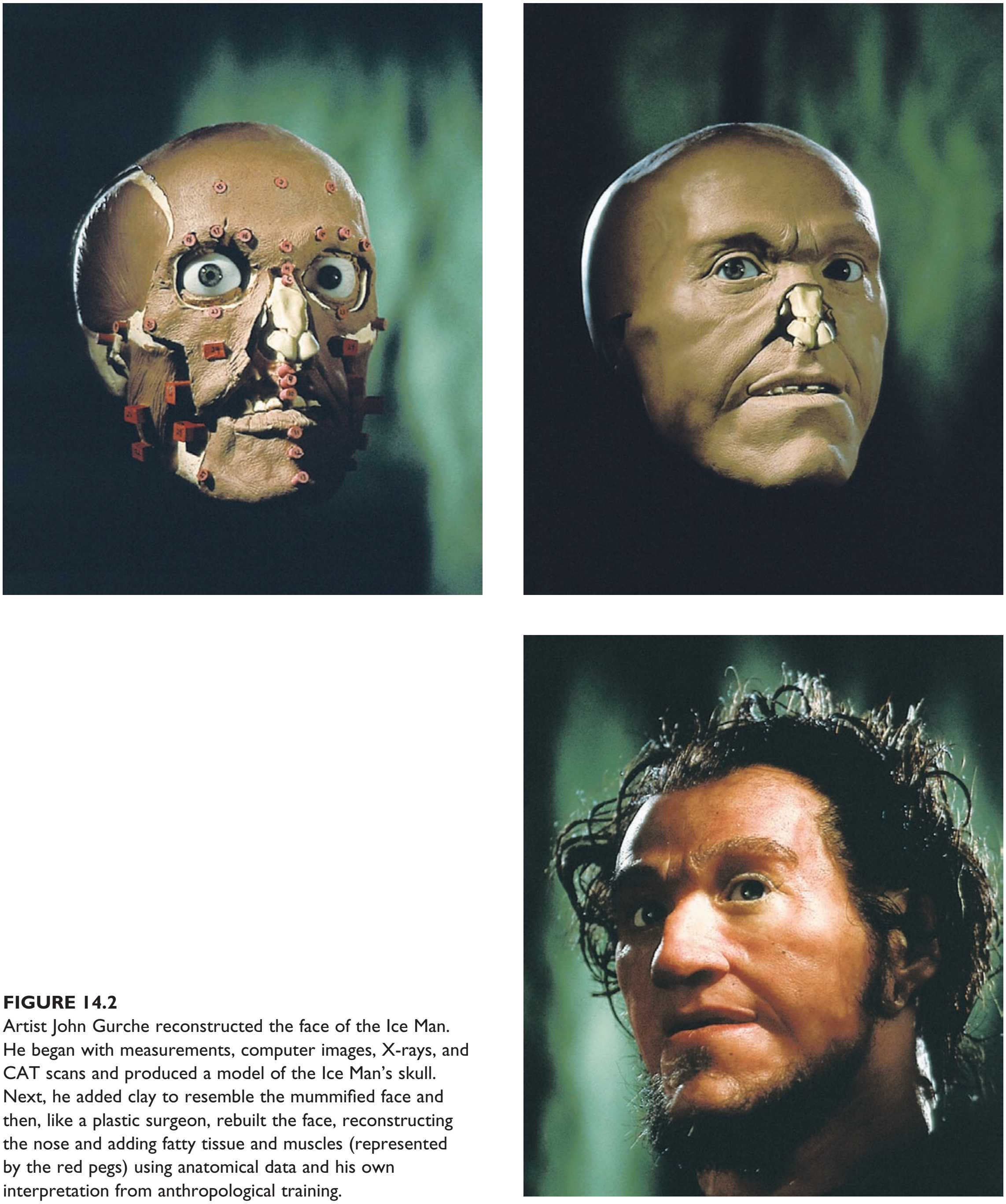


FIGURE 14.2
Artist John Gurche reconstructed the face of the Ice Man. He began with measurements, computer images, X-rays, and CAT scans and produced a model of the Ice Man's skull. Next, he added clay to resemble the mummified face and then, like a plastic surgeon, rebuilt the face, reconstructing the nose and adding fatty tissue and muscles (represented by the red pegs) using anatomical data and his own interpretation from anthropological training.

suggestion (see Wong 2010) is that he died there and was ceremonially buried up on the mountain.

All the preceding information and more can be gleaned from a mummified corpse over fifty centuries old. When the Ice Man died, writing was just being invented in Mesopotamia, the great pyramids of Egypt had yet to be built, and the lives of Julius Caesar and Jesus were over 3,000 years in the future.

As famous as the Ice Man is, we do not, of course, know his name. Forensic studies, however, have provided us with new information about some famous people whose names we do know. For example, the late forensic anthropologist William Maples (Maples and Browning 1994) helped identify the skeletal remains of the assassinated Russian czar Nicholas II and his family. (The bones did not, by the way, include those of Anastasia, the czar's daughter, said to have survived and escaped to the West.) Maples also examined the remains of U.S. president Zachary Taylor to prove that he was not murdered by arsenic poisoning. He also helped identify the true remains of Spanish conquistador Francisco Pizarro and proved that a mummy reported to be Pizarro's was actually someone else's.

Clyde Snow, another well-known forensic anthropologist, identified a skeleton found in Brazil as that of Nazi war criminal Josef Mengele. The standard information about the skeleton fit what was known about Mengele, but Snow clinched it by superimposing images of the skull over photographs of the man known as the "Angel of Death." They matched, and the identification was verified shortly thereafter, when Mengele's dental records were discovered. Snow has also been involved in a review of the assassination of John F. Kennedy and has searched in Bolivia for the remains of the famous outlaws Butch Cassidy and the Sundance Kid, so far without success.

More important, however, than these cases of the rich or famous are those involving the remains of common, everyday people who, for one reason or another, need to be identified and who, perhaps, require justice. Clyde Snow has, for example, examined and tried to identify the remains of some of the more than 10,000 people who "disappeared" during the military rule in Argentina from 1976 to 1983. His evidence has been used to help prosecute some of those responsible. He has done similar work in the Philippines and in Southwest Asia, and he has helped identify the victims of airline crashes, including one that took place in Chicago in 1979 that killed 273 people. And we've already mentioned Amy Mundorff's work at the World Trade Center.

Investigating smaller tragedies, however, is not outside the activities of the forensic anthropologist. For a typical example, we can look at one of Clyde Snow's cases (Snow and Luke 1970). In the summer of 1967, two young girls, ages 5 and 6, disappeared in the Oklahoma City area within a few weeks of one another. In November of that year, two hunters found some bones, including a human cranium, in a rural area outside the city. The bones were scattered on the surface of the ground. Further investigation, however, revealed a crude grave that contained more bones and children's clothing. An extensive excavation was conducted. Among the several hundred bones eventually recovered—most of which belonged to various nonhumans—were those of a young child. Snow investigated further to see if the bones could reveal a specific identity and perhaps a cause of death. There was a good chance that these were the bones of one of the missing girls, and perhaps even both.

Snow determined that the bones had been buried fairly recently. They still had the greasy texture of fresh bone, and there were no signs of weathering that would indicate they had been there over winter. Although the bones had been damaged by scavengers, there were no rodent gnaw marks on them (rodents gnaw well-weathered bones for minerals and protein). The bones were recent, but how recent?

They were completely skeletonized, but this could certainly have happened during the previous summer. It was shown that in Oklahoma's climate, a child's body would be reduced to bone within 2 to 6 weeks. There were spider webs and other signs of insect activity in the skull, so it was determined that the bones had been completely exposed before cold weather set in and those creatures became inactive. Burial had occurred in early September at the latest.

Soon, the possibility that more than one human was represented was ruled out. The cause of death was a problem, though. Much of the skeleton was missing, and the bones that remained were found scattered about. Some bones were damaged, and some teeth were missing. None of this, however, could be clearly attributed to trauma before death or purposeful dismemberment afterward. More likely, it was the result of decomposition and the work of carnivorous scavengers that dug up the grave, scattered the bones, and carried off those with fleshy parts.

Determining the sex of the skeleton was difficult. No pelvis was found, nor was there enough of the remainder of the skeleton to make a good assessment for a preadolescent. The clothing found was that of a little girl, however.

Both of the missing girls were white, and the presence of some dental features pointed to that population. Age was determined through cranial sutures, epiphyseal union, and dental eruption and development (see Chapter 9). Tooth eruption narrowed the age range to about 6 to 8 years. The evidence, then, favored the skeleton being that of the older missing girl. Finally, stature was estimated using formulas that compare the length of various long bones to total height. The skeleton was estimated to have belonged to someone about 50 inches tall. The older missing girl was about that height, while the younger was 8 inches shorter.

Snow concluded that the remains probably belonged to one of the two missing girls. There had been no other unsolved cases of missing girls of that age from the area in several years. The bones most likely were those of the 6-year-old. Sadly, the remains of the other girl have not been found, and no suspect has been identified. But Snow's forensic work helped strengthen the identification, which would have been little more than a good guess without the precise information he was able to extract by reading the bones.

LESSONS FROM THE PAST

Besides applying the skills of the biological anthropologist to legal matters, we may also apply the perspective of our discipline to areas of modern life. Humans are variations on the primate theme. We retain many of the major primate characteristics, and our unique features are still based on them. Moreover, in no way can we say that the modern manifestation of our species is the culmination or the best-adapted form of our evolutionary line. We have manipulated our environment, our very biology, and our behavior through culture, so our present environment may not be the one to which our species was biologically adapted. We may well learn a few valuable lessons by taking a closer look at what we were like in the past, before culture played so great a part in our lives.

For instance, anthropologists Marcia Thompson and David Harsha (1984) have looked at the daily routines of people in modern industrial societies and compared them with those of people in nonindustrial cultures and nonhumans living in the tropics. They conclude that in the common structure of our workdays, we are violating a pattern that evolved in our tropical ancestors and cousins that programs us for a two-peaked rhythm of daily activity, one peak in the late morning and another in the late afternoon, with a lull in between. That period of tiredness we often feel after lunch may have nothing to do with eating.

Tropical animals and people in many human societies take an afternoon break. Originally, this break may have been a response to the heat of the midafternoon sun, but as we are coming to understand it, this behavior may reflect a real biological decrease in human activity level. After all, other bodily functions—more than a hundred physiological and performance variables—fluctuate in predictable cycles during the twenty-four hours of our day. Thus, the afternoon nap is a natural phenomenon. (I knew it!)

Thompson and Harsha suggest that the best way to respond to this fluctuation—given that most of us can't nap, at least during weekdays—would be to move lunch back a few hours to correspond to the afternoon lull. As it is, we often take lunch during one of our peak activity periods. By taking into account a possible biological pattern, we might make ourselves more productive in our modern cultural environment.

Another anthropologist, James McKenna (1996), has looked at the sleep behavior of other primate groups and of people in cultures in which it is common for young babies to sleep with their parents. In the West, we have long been advised that babies should sleep by themselves, probably as a response to our emphasis on independence and the idea that the parents' lives, perhaps especially in bed, are separate from those of their children.

McKenna suggests that, in fact, infant nonhuman primates and human babies seem better off psychologically and physically if they sleep with their parents. In humans, this may even extend to learning to breathe properly. You may think of breathing as an involuntary action, but our unique ability to speak requires that we humans use two kinds of breathing—automatic and controlled. And the ability to switch between these two kinds of breathing is learned. In addition, remember that the vocal tract of human infants is initially higher than that of adult humans and similar to that of chimpanzees. As the vocal tract begins to drop early in life, the baby goes through a great physical change.

These two facts—the development of the two kinds of breathing and the physical change in the vocal tract—may explain sudden infant death syndrome (SIDS), when babies inexplicably die in their sleep. It is thought that miscues in regulating breathing cause these babies to stop breathing and prevent them from waking themselves up so they can start breathing again. Sleeping with a parent, McKenna argues, may help prevent SIDS, because the parent's movement causes the baby to wake up periodically, and so the infant learns better how to switch between the two kinds of breathing. McKenna notes that SIDS is twice as common in the United States as in Japan, where infants normally sleep with their parents. A more recent study (Mosko et al. 1997) has also suggested that close proximity to the mother while sleeping, especially sleeping face-to-face, may also provide the infant with increased levels of CO_2 from the mother's respiration, which might help stimulate its breathing.

Finally, S. Boyd Eaton and Melvin Konner propose that the major chronic illnesses that we in the industrialized West suffer from are caused by a "mismatch between our genetic constitution" and various factors in our modern lifestyles, including diet, exercise, and exposure to such things as alcohol and tobacco. Our genes, they suggest, "must now function in a foreign and, in many ways, hostile Atomic Age [environment]" (1985:1).

They note that some studies indicate that our ancestors who lived before the advent of farming, about 12,000 ya, were taller and more heavily muscled than we are. Their teeth also showed a much smaller percentage of dental caries (tooth decay). The authors suggest that by looking at the lives of recent hunter-gatherer groups, we may have a "window" into the world of our Stone Age ancestors (Figure 14.3). (They are careful, of course, to caution that recent hunter-gatherer groups are fully modern humans with technologies, such as the bow and arrow, that were not available until about 15,000 ya.) One thing we note right away is that such people have a lower incidence of coronary disease, emphysema, hypertension (high blood pressure), and cancers of the breast, prostate, colon, and lung.

When the diets of fifty hunter-gatherer groups were analyzed, it was seen that, on average, they ate more red meat than we do now. This doesn't sound like a healthy diet at first, until we understand that wild game has much less saturated fat than do domestic animals and that most of that is "structural" fat (rather than "storage" fat), which is largely polyunsaturated—not the harmful kind. Thus, our ancestors ate about three times the protein we do but only about half the fat.

Because most of the plant foods eaten were wild and unprocessed, they had a higher nutritional value, fewer calories, more complex carbohydrates (rather than simple ones that turn to fat), more fiber, and less salt (a contributor to hypertension). Furthermore, our ancestors drank mostly water and seldom were exposed to alcohol and tobacco.

Additionally, rather than concentrating on one sort of exercise, our ancestors were more like "decathlon athletes," responding to the harsh

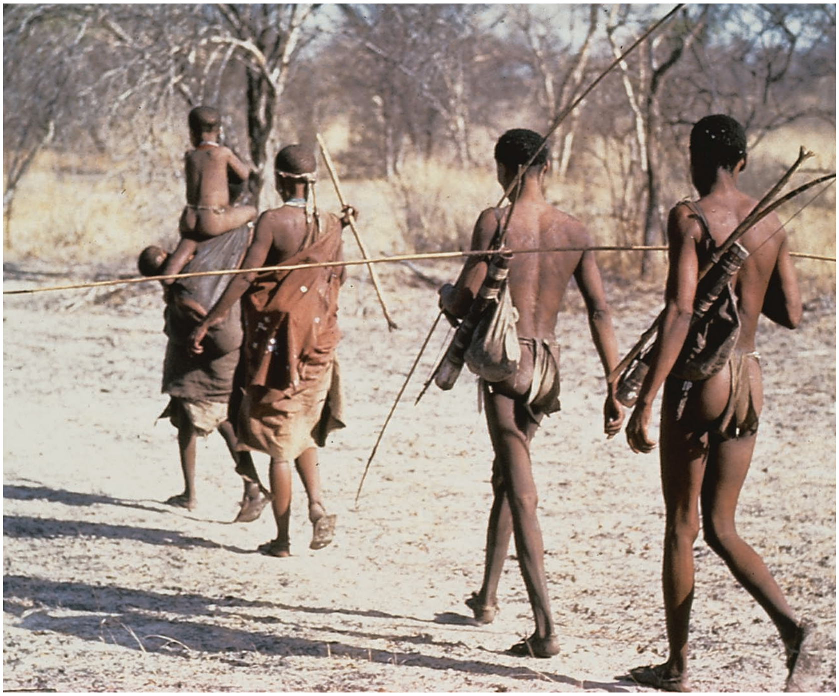


FIGURE 14.3
The Ju/'hoansi, a population of Khoisan peoples from the Kalahari Desert in Namibia, Botswana, and South Africa, are, of course, fully modern humans. Yet their way of life, until recently that of hunters and gatherers, can give us a window into the lives of our ancestors before the invention of farming and animal domestication. Here, members of a Ju/'hoansi family are on the move, carrying with them their children, tools, weapons, and other possessions. The lives of the Ju/'hoansi, and of all Khoisan, have been changed forever by political and military events in southern Africa since this photo was taken over forty years ago.

physical demands of their lives with a varied "exercise program" that changed daily and seasonally.

As an example of this, a study (Cooper et al. 1999) compared rates of hypertension in subjects from Nigeria (7 percent), Jamaica (26 percent), and Chicago (33 percent; all of the subjects from Chicago were African American). The subjects sampled shared, on average, 75 percent of their genes (probably more; this study was done before the genome was sequenced), so major genetic differences were ruled out. Rather, differences in lifestyle, diet, and exercise were suggested as accounting for 40 to 50 percent of the increased risk for hypertension characteristic of African Americans over Nigerians. Specifically, by comparison, African Americans were more prone to being overweight, getting little exercise, and having a poor diet that included a high level of salt.

The lessons from this research are obvious and are, indeed, suggestions we hear all the time. We know we're supposed to eat low-fat foods, cut down on salt, get plenty of fiber, and exercise regularly. Evolution, though, provides an explanation and rationale for following those suggestions.

Contemporary Reflections

What Can One Do with a Degree in Bioanthropology?

It's safe to say that most people who work as professional biological anthropologists (or, for that matter, any sort of professional anthropologist) have at least a master's degree and, more likely, a PhD. The majority of these do what I do—teach in a college or university while researching and writing. Although acquiring a PhD requires, on average, four additional years of university classwork and a variable number of years after that to complete a doctoral dissertation (I took six years), it is a career I can highly recommend. Essentially, you get paid to learn about and think about the subject you're most interested in and then to impart that knowledge to your students and apply it to science and society. It entails a good deal of (often inconsequential) committee work and other related activities, but all in all it's a very rewarding life.

Unfortunately, at the moment there are more PhD's and near PhD's in anthropology than there are university faculty jobs. The job market, however, has improved and worsened several times in the thirty-nine years I've worked at my university, and the situation could improve again. You shouldn't let current conditions dissuade you if a PhD and a university position are your goal.

Some bioanthropology PhD's work in other departments of universities. It is not uncommon to find them in medical, dental, and nursing programs, or in biology, genetics, psychology, public health, or physical therapy departments. Others work outside academia. I glanced through the list of current members of the American Association of Physical Anthropologists and found people who work for museums, medical research and forensics institutes, the armed forces, and government agencies such as the Bureau of Land Management. As I mentioned, the Connecticut State Archaeologist is a former student of mine who has his PhD in bioanthropology.

BIOANTHROPOLOGY AND GLOBAL ISSUES

Global issues are global in two senses: (1) they affect a wide geographic range and a large number of people, and (2) they involve many different aspects in a complex set of interrelationships. Biological anthropology can neither address in detail all those aspects nor hope to solve any of these problems alone. But the perspective of bioanthropology—its evolutionary and holistic point of view—can help us gain insight into some of these issues and can certainly make a contribution as we seek responses and possible solutions.

In Chapter 12 we examined in some detail one global issue, emerging diseases. Another issue of major concern is global climate change, popularly called global warming. Although there is still some debate on the existence of this phenomenon, the dissent is economically or politically motivated. People, corporations, and governments don't *want* global

Most of you reading this book, however—if you are working toward a degree in anthropology—will get a BA. It has been said that one bachelor's degree is as good as another in terms of finding jobs that require a college education. On a practical level, that may well be true. What a four-year degree means is that you have shown mastery of a certain core curriculum at a certain level with a focus on a particular discipline and that you had the skills, dedication, and persistence to achieve that degree. In terms of specific skills needed for a certain job, the college degree essentially tells an employer that you will have the ability to learn and use those skills.

But *what* degree you get may have deeper meaning, and—although I'm clearly biased—I think a degree in biological anthropology is a good choice. The breadth of knowledge inherent in the field is wide. There is the focus on scientific methodology but with the need—because it *is* anthropology—to understand other areas of knowledge and other cultures. The central theme of evolution necessarily involves a deep understanding of biology in general and of the biology of other species in particular. Genetics, anatomy, physiology, behavior, ecology, chemistry and physics (for dating techniques), geology, paleontology, and medical topics are all integral parts of the field. The number of careers to which such topics, such a breadth of knowledge, and such a perspective could be applied is huge—limited only by your imagination.

The only barrier might be the fact that many people have little understanding of what bioanthropology is and so might not at first think such a degree would be appropriate for certain jobs. I tell my students that in such instances they must be prepared to make their case, to explain to potential employers what bioanthropology is and why that background would be ideal for their job.

For some sound practical advice, read *Careers in Anthropology*, by John T. Omohundro (2001). In the meantime, the answer to the question about what you can do with a degree in bioanthropology is, just about anything you want.

warming to be acknowledged because having to deal with it will adversely affect them. However, scientists have not doubted for many years that global warming is a real trend (Epstein 2000).

Even in these areas of practical concern, however, anthropology in general can play a role. We humans will have to make adjustments if we are to slow, much less reverse, the warming trend. Changes in energy use, consumption of resources, waste disposal, and transportation habits will affect everyone—from the individual consumer to the largest multinational corporation. And even changes brought about initially by one nation will have effects on other nations, because we truly live in a global economy and a global environment. Anthropology can help predict what ramifications such changes will have on individual cultural systems and on the relationships among different cultural systems.

Some of the potential results of global warming relate directly to the subjects we've covered in this book. Genus *Homo* has dealt with climate change since first appearing on the planet, but global warming threatens to produce changes at a much more rapid rate than before. Furthermore, it must be understood that the modern world we know has come about in just the past few hundred years; during this time we have not seen climate change of the scale predicted. In other words, modern cultures have adapted to a relatively unchanging set of environments and could be severely disrupted by the more sudden changes that computer models of global warming project.

For example, if warming continues, ocean temperatures will increase and polar ice caps and glaciers will melt (this is already happening). This will cause sea levels to rise and thus flood coastal areas, where populations tend to be concentrated. As a result, large numbers of people will have to move. The influx of saltwater will destroy crops and natural plants and render land unusable for agriculture. There will be severe heat waves, which will produce droughts, heat-related deaths, and an increase in smog production. (These, too, are already happening.)

Global warming will also have an impact on disease. As climates warm, disease-causing and disease-carrying organisms will expand their ranges. Already there have been cases of West Nile virus in New England and malaria in Toronto, as the associated mosquito species move into regions formerly inhospitable to them. Rodent-borne disease will also increase as those highly adaptable mammals expand their ranges, aided by decreases in predator populations as climates change. Dryness will cause major fires, which will add to pollution-caused ailments.

The risks are many and multifaceted. The perspective of biological anthropology—looking for connections, seeing our species as a biological/cultural system adapted to environmental systems—is a valuable one for understanding the causes and ramifications of global warming and for suggesting and implementing ways of dealing with them.

While the theoretical issues covered in this book are interesting in and of themselves, I believe they also make anthropology uniquely qualified to play a role in these and other global concerns. Indeed, I think we as anthropologists are obligated to do so.

SUMMARY

Biological anthropology studies the human species, past and present, from the perspective of evolutionary processes, change, and adaptation. To understand how these forces affected our ancestors, we have developed technologies that allow us to squeeze an amazing amount of information out of the meager skeletal remains that those ancestors left us. These skills are now being increasingly recognized and used by law enforcement agencies in the identification and analysis of skeletal remains of missing persons and accident and murder victims. Forensic anthropology is a fast-growing specialty within our field.

Our evolutionary perspective can also be useful in more abstract ways. By understanding the nature of our adaptations as a species, we may evaluate some of our behaviors and practices in light of the recent cultural environment we have made for ourselves. We find that some of our cultural adaptations may be out of step with our biological ones. Using the evolutionary viewpoint to look at daily biological rhythms, sleep patterns, the nature of our breathing, diseases that affect us, our diet, and our exercise habits—among other aspects of our lives—may enable us to adopt behaviors that are more in line with how our species is actually adapted and, in so doing, improve our lives.

Biological anthropology may also be applied to modern global issues such as emerging diseases (see Chapter 12.) Even something as seemingly removed from anthropology as global warming can be examined from anthropology's holistic and evolutionary perspectives.

In the end, however, it must be noted that to be useful and important, knowledge need not have a practical, concrete application. There is nothing wrong with the idea of knowledge for its own sake, and, certainly, learning about our species—where we came from, what processes brought about our evolution, who we are, and where we fit in the natural world—should be important to us as individuals and as members of our own society and the society of all the world's peoples.

QUESTIONS FOR FURTHER THOUGHT

1. What other issues of personal health and lifestyle do you think bioanthropology could address? How might the perspective of this discipline add something that other fields might have missed?
2. Within or resulting from the major issues of emerging diseases and global warming are other matters of concern: pollution, population, deforestation and other examples of environmental destruction, and warfare between nations, religions, and ethnic groups. How might anthropology, especially biological anthropology, shed some light on these issues? What avenues of research would be opened up by applying bioanthropology to these cases?

3. In Chapter 13, we concluded that biological races do not exist for the human species. But on page 353 of this chapter, I describe the use of racial categories and biological traits in the identification of the two missing girls from Oklahoma. Is this contradictory? If not, why?
4. Finally, a real challenge. The nature of the real world certainly influences religious, philosophical, and ethical ideas. Consider some current ethical debates—abortion, euthanasia, stem cell research, for example—and ask whether the perspective of bioanthropology and the facts about the real world that our science has discerned might contribute to the direction and possible resolution of these debates.

SUGGESTED READINGS

The June 1993 issue of *National Geographic* includes an article, "The Ice Man," by David Roberts, that covers the Ice Man as well as some of the related archaeology of his time and place. See also "The Iceman Reconsidered," by James Dickson, Klaus Oeggl, and Linda Handley, in the May 2003 *Scientific American*.

Two finds of mummified bodies have been reported from western China and from Peru. See "The Silk Road's Lost World," by Thomas B. Allen, in the March 1996 *National Geographic*, and three articles by Johan Reinhard in the June 1996, January 1997, and November 1999 issues of the same magazine.

More on the reconstruction of ancient faces can be found in John Prag and Richard Neave's *Making Faces*.

On forensic anthropology, see *Dead Men Do Tell Tales*, by William R. Maples and Michael Browning; *Bones: A Forensic Detective's Casebook*, by Douglas Ubelaker and Henry Scammell; *Flesh and Bone*, by Myriam Nafte; *Bone Voyage*, by Stanley Rhine; and *No Bone Unturned: The Adventures of a Top Smithsonian Forensic Scientist and the Legal Battle for America's Oldest Skeletons*, by Jeff Benedict. The latter is about anthropologist Doug Owsley and includes an update on the Kennewick Man story. See also two articles in the 11 August 2000 issue of *Science*: "A New Breed of High-Tech Detectives," by Andrew Watson, and "Where Dead Men Really Do Tell Tales," by Robert Service.

The Clyde Snow case covered in this chapter is recounted in detail in "The Oklahoma City Child Disappearances," by Snow and James Luke, in Aaron Podolefsky and Peter Brown's *Applying Anthropology*. A profile of Snow appears in the December 1988 issue of *Discover* in a piece by Patrick Huyghe, "No Bone Unturned."

The global warming situation is nicely discussed in "Is Global Warming Harmful to Health?" by Paul R. Epstein in the August 2000 *Scientific American*.

For an interesting look at broad ecological issues as they relate to human societies, see Jared Diamond's *Collapse: How Societies Choose to Fail or Succeed*.

APPENDIX I

Protein Synthesis and the Genetic Code

How does protein synthesis work? As you read this description, follow along in the figure on page 365. During protein synthesis, only a portion of the DNA molecule is unwound (in contrast to the complete unwinding seen in replication). **Messenger ribonucleic acid (mRNA)** is assembled against one strand of this unwound DNA. (Only one strand carries the code; the other is structural.) The mRNA **transcribes** the gene by matching complementary bases to those exposed in the coding strand of DNA, except that uracil (U) replaces thymine (T).

After mRNA has transcribed the code, it leaves the nucleus of the cell and moves to specialized structures in the cell called *ribosomes*, where the message is decoded and **translated** into an actual protein. Another type of RNA called **transfer RNA (tRNA)** reads the three-letter codes, or codons, as instructions for assembling a chain of amino acids. Each set of three exposed RNA bases codes for one amino acid. Thus, for example, a sequence of 300 bases codes for a sequence of 100 amino acids. A sequence of amino acids is a protein. Although there are only about twenty or so types of amino acids, it is possible to arrange them in a nearly infinite variety of sequences and lengths. In this way, the sequence of DNA bases represents a sequence of amino acids, and it is this sequence that determines the shape and function of the protein.

What does the code look like in terms of the codons for the amino acids? Because there are four bases (letters) in the genetic alphabet that make codons in three-letter combinations, there are sixty-four (4^3) possible codons. But there are only twenty amino acids used to make our proteins. Look at the table on page 366.

Note that most amino acids can be coded for by more than one codon. Valine, for example, is coded for by CAA, CAT, CAC, or CAG. Notice also that it is the first two bases that make up the code; the third is, in this case, irrelevant. These four codons are said to be "synonymous," since they code for the same amino acid. This system has evolved to take into account some of the possible errors that can occur during protein synthesis. In addition, some of the codons are "stop" codons, acting as punctuation.

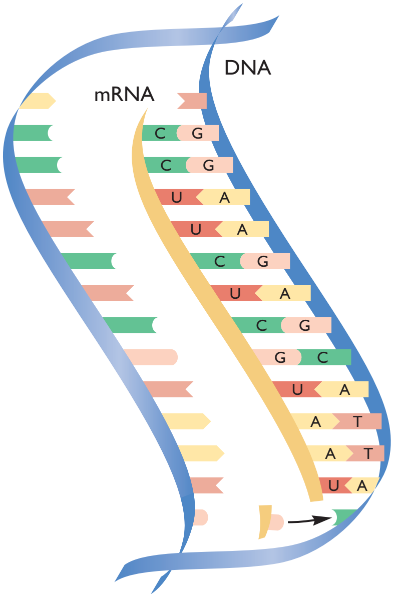
messenger ribonucleic acid (mRNA) The molecule that carries the genetic code out of the nucleus for translation into proteins.

transcription The process during which mRNA is formed from the DNA code.

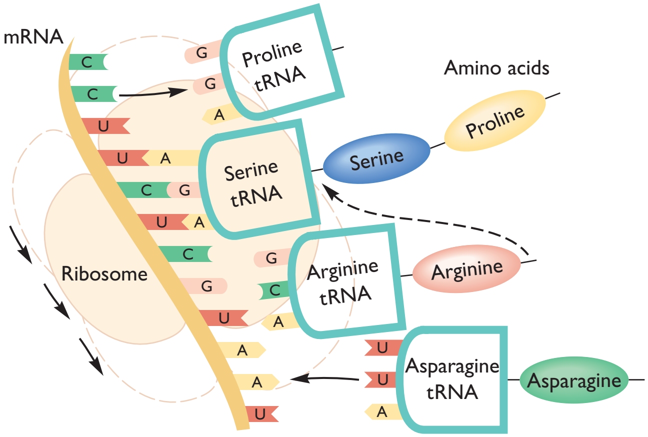
translation The process during which the mRNA code builds a protein using amino acids supplied by tRNA.

transfer ribonucleic acid (tRNA) RNA that lines up amino acids along mRNA to make proteins.

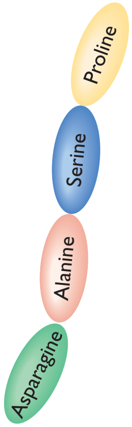
1. DNA molecule temporarily separates at bases. mRNA lines up its bases (with U replacing T) with their complements on the coding side of the DNA.


DNA
mRNA
C G
C G
U A
U A
C G
U A
C G
G C
U A
A T
A T
U A

2. mRNA moves out of cell nucleus to ribosomes. As ribosomes move along mRNA, tRNA picks up amino acids and lines up along mRNA according to base complements. Each tRNA transfers its amino acid to the next active tRNA as it leaves, resulting in a chain of amino acids.


mRNA
Proline tRNA
Amino acids
Proline
Serine
Serine tRNA
Ribosome
Arginine tRNA
Arginine
Asparagine tRNA
Asparagine
C G
C G
U A
U A
C G
U A
C G
G C
U A
A U
A U
U A

3. This chain of amino acids forms a protein. In reality, no protein is only four amino acids long, but the process works exactly as shown.


Proline
Serine
Alanine
Asparagine

First Base	**Second Base**			
	A	***T***	***C***	***G***
A	AAA Phenylalanine	ATA Tyrosine	ACA Cysteine	AGA Serine
	AAT Leucine	ATT Stop	ACT Stop	AGT Serine
	AAC Leucine	ATC Stop	ACC Tryptophan	AGC Serine
	AAG Phenylalanine	ATG Tyrosine	ACG Cysteine	AGG Serine
T	TAA Isoleucine	TTA Asparagine	TCA Serine	TGA Threonine
	TAT Isoleucine	TTT Lysine	TCT Arginine	TGT Threonine
	TAC Methionine	TTC Lysine	TCC Arginine	TGC Threonine
	TAG Isoleucine	TTG Asparagine	TCG Serine	TGG Threonine
C	CAA Valine	CTA Aspartic acid	CCA Glycine	CGA Alanine
	CAT Valine	CTT Glutamic acid	CCT Glycine	CGT Alanine
	CAC Valine	CTC Glutamic acid	CCC Glycine	CGC Alanine
	CAG Valine	CTG Aspartic acid	CCG Glycine	CGG Alanine
G	GAA Leucine	GTA Histidine	GCA Arginine	GGA Proline
	GAT Leucine	GTT Glutamine	GCT Arginine	GGT Proline
	GAC Leucine	GTC Glutamine	GCC Arginine	GGC Proline
	GAG Leucine	GTG Histidine	GCG Arginine	GGG Proline

It should be noted, however, that not all synonymous codons have the same results. The specific codon may not change the amino acid, but it might change how fast a protein is made and how much of a protein a cell can make, and it can affect the shape of the mRNA molecule (Judson 2008).

APPENDIX II

Genes in Populations

The genetic definition of evolution is *change in allele frequency over time*. Therefore, evolution entails any process that alters the frequencies with which alleles of genes appear in a population. We can use the concept of allele frequency more specifically by applying actual allele frequency numbers in our study of human evolution.

The example of evolution we focused on in Chapter 4 was sickle cell anemia. Let's continue with that example. Suppose we can test a population for the sickle cell genotypes at two points in time. Our first test gives the following numbers:

AA (normal hemoglobin)	50 people
AS (sickle cell trait)	100 people
SS (sickle cell anemia)	50 people
Total	200 people

(A and S are *alleles of a single gene*, the *Hb* gene for hemoglobin.)

Now, when we return to test the population at some point in the future, we find the following numbers:

AA	35 people
AS	100 people
SS	10 people
Total	145 people

Obviously, some change has taken place in the frequency of the genotypes and in the total population size. Have allele frequencies changed as well? In other words, has evolution, by the genetic definition, taken place? To calculate the allele frequencies, we add up the total number of each allele and divide by the number of alleles in the population, which would be twice the number of people, since each person has two alleles at each locus. Thus, for the first test, the number of A alleles is

$(50 \times 2) + 100 = 200$ (since each AA person has two A alleles and each AS heterozygote has one)

allele frequency The percentage of times a particular allele appears in a population. Another name, and the preferred term, for gene frequency.

The frequency of A alleles in the population is thus

200/400 (since each of the 200 people has two alleles = .50 (50%)

Using the same reasoning, the frequency of the S allele is also .50 (50%).

Now, let's calculate the allele frequencies in the second test, after the obvious changes in genotype frequency and number of people have taken place. Using the same procedure:

frequency of A × ([35 × 2] + 100) / (145 × 2) = .59 (59%)
frequency of S = ([10 × 2] + 100) / (145 × 2) = .41 (41%)

(The results are rounded for simplicity.) Thus, the frequency of the A allele has increased and that of the S allele has decreased. Evolution, by technical definition, is taking place.

The reason for this change is obvious because we understand sickle cell anemia. Those individuals with the SS genotype have a fatal disease, so only 20 percent (10 out of 50) of them survived between the two tests. Those with the AA genotype don't have sickle cell, but some may have succumbed to malaria; here there was a 70 percent survival rate (35 out of 50) for the AA genotype. All of the heterozygotes survived since they have nonfatal symptoms of sickle cell and also possess an immunity to malaria.

If, however, we did not already understand the situation, the calculation of these figures would show that *something* was happening and would indicate in which direction the change was taking place. It would be clear in this case that one allele is increasing in frequency because both homozygote genotypes are decreasing in number, but to different degrees. As a result of *this*, the heterozygote genotype is becoming more common. We would then try to figure out why.

Suppose, however, we could examine the population only once, as is often the case. How could we possibly see evidence for change over time? There is a formula, known as the Hardy-Weinberg equilibrium, that provides us with a tool to do this. The formula is an example of a *null hypothesis*, a condition where nothing occurs. If you can state the conditions of *no* change, you can then compare them to a real situation and see whether change is taking place and, if it is, state the nature and direction of that change. The Hardy-Weinberg formula assumes that the genotype frequencies in a population will remain the same under certain conditions: (1) if mating is random (that is, everyone stands an equal chance of mating with anyone else of the opposite sex), and (2) if there is no gene flow, no drift, no mutation, and no natural selection for any allele over another. In other words, none of the processes of evolution are taking place.

For example, using our two alleles for hemoglobin, A and S, we designate the frequency of A as p and the frequency of S as q. (These letters, although they may make it a bit confusing at first, are used because of a mathematical convention.) So, for our population in the second test above:

$p = .59$ and $q = .41$

Now, we calculate the probability (the chance) of creating each of the three possible genotypes *based solely on the percentages of the two alleles*. The probability is the product (the result of multiplication) of the frequencies of the alleles that make up each genotype. How often a genotype is produced depends on how often the alleles of that genotype appear in the first place. Thus, the following applies:

Genotype	Product of Frequencies	
AA	$p \times p = p^2$	
AS	$p \times q = pq$	$= 2pq$
SA	$q \times p = qp$	
SS	$q \times q = q^2$	

The heterozygote is counted twice because there are two ways of producing it, depending on which allele comes from which parent. Because all genotypes are now accounted for,

$p^2 + 2pq + q^2 = 1$ (or 100 percent)

This is the Hardy-Weinberg formula for a two-allele gene.

We can now return to our population and see what its genotype frequencies would be if they were based only on the frequencies of the alleles, that is, if there were no evolutionary processes taking place and the percentages of the genotypes were strictly a matter of chance. For the AA genotype, for example, we calculate p^2 as $.59 \times .59 = .3481$. Next, we multiply this by the population size, 145, to show how many people would be *expected* to have this genotype if no evolution were taking place: $145 \times .3481 = 50$. Looking back, however, we observe that only 35 people actually possessed this genotype. We can do the rest of the calculations, producing the following results:

Genotype	Expected Frequency	Expected Number	Observed Number
AA	$p^2 = .59^2 = .3481$	$.3481 \times 145 = 50$	35
AS	$2pq = 2 \times .59 \times .41 = .4838$	$.4838 \times 145 = 70$	100
SS	$q^2 = .41^2 = .1681$	$.1681 \times 145 = 24$	10

(The "expected number" and "observed number" columns should each add up to 145, but the former doesn't exactly because of rounding.)

The results are based on chance alone: the observed number of people possessing each genotype is not the same as the expected number. In evolutionary terms, then, our sample population is not in Hardy-Weinberg equilibrium. Something else is going on; namely, some evolutionary processes are in action.

In real life, we would still have to run certain statistical tests on our results, because the fact that the expected and observed numbers do not match could still be the result of chance. For the record, I ran a chi-square (a test of statistical significance) and found that the above results are not a matter of chance. They are, therefore, in mathematical terms, statistically significant.

At any rate, we can note the direction of the differences. Again, comparing expected with observed frequencies, we see that there are large drops in the numbers of people with the AA and SS genotypes and a large increase in those with the AS genotype. This hints that the heterozygote is being selected for and that the two homozygotes are being selected against. We know, of course, that this is the case with sickle cell anemia in malarial areas.

The other processes of evolution may also be quantified and studied in a similar fashion—by observing changes in allele frequencies over time or by calculating deviations from Hardy-Weinberg equilibrium—and then by noting the direction of change and determining the probable causes of that change.

GLOSSARY OF HUMAN AND NONHUMAN PRIMATES

Adapidae (*ah-da'-pih-day*) A group of early primates from the previously connected landmass of North America and Europe, dating to more than 50 mya and thought to be ancestral to prosimians such as lemurs and lorises.

Aegyptopithecus (*ee-gip'-tow-pith'-ah-cuss*) An extinct monkey genus with several apelike traits. Discovered in Egypt and dated at approximately 34 mya, it may represent a form of primate ancestral to Old World monkeys and apes.

Anthropoidea (*an-throw-poy'-dee-ah*) According to the traditional taxonomic system, one of the two suborders of order Primates (the other is Prosimii). Means "humanlike" and includes monkeys, apes, and humans.

Ardipithecus kadabba (*ar-di-pith'-ah-cuss kah-dah'-bah*) An earlier species of *Ardipithecus* from Ethiopia and dated at 5.8 to 5.2 mya; interpreted by some as bipedal. The subspecies name means "base family ancestor" in the Afar language.

Ardipithecus ramidus (*ar-di-pith'-ah-cuss rah'-mi-dus*) A hominid species from Ethiopia and dated at about 4.4 mya, based on skeletal fragments and teeth. Not yet fully documented or accepted, it is thought by its discoverers to represent one of the earliest species in the hominid line; thus the species name, which means "root" in the local language.

Australopithecus afarensis (*os-trail-oh-pith'-ah-cuss ah-far-en'-sis*) A fossil species from East Africa, the oldest well-established species in the hominid line. Dated at 3.9 to 3 mya, *afarensis* had a small, chimp-sized brain but walked fully upright.

Australopithecus africanus (*os-trail-oh-pith'-ah-cuss ah-frih-cane'-us*) A fossil hominid species from South Africa dated from about 3 to 2.3 mya. It is similar to A. *afarensis* and may well be a direct evolutionary descendant of the earlier species. It retained the chimp-sized brain and was fully bipedal.

Australopithecus anamensis (*os-trail-oh-pith'-ah-cuss ah-nah-men'-sis*) The earliest well-documented fully bipedal hominid found in Kenya and dating from 4.2 to 3.8 mya.

Australopithecus bahrelghazalia (*os-trail-oh-pith'-ah-cuss bar-el-gah-zahl-ya*) A new species of this genus, based on a jaw and several teeth found in Chad and dated at 3.5 to 3 mya. The species name is derived from an Arabic name for a nearby riverbed. It is noteworthy as the only early hominid found outside of East Africa or southern Africa.

Australopithecus garhi (*os-trail-oh-pith'-ah-cuss gar'-hee*) Recently discovered fossils from Ethiopia, dated at 2.5 mya, that display resemblances to both *Australopithecus afarensis* and early *Homo*, leading some authorities to consider them a new species and a direct ancestor of *Homo*.

Australopithecus sediba (*os-trail-oh-pith-ah-cuss seh-dih-bah*) Recently discovered hominid from South Africa, dated about 2 mya. Said by discoverers to be a good candidate for the specific ancestor of *Homo*.

Catarrhini (*cat-ah-rine'-eye*) One of two infraorders of suborder Anthropoidea (the other is infraorder Platyrrhini, the New World monkeys). Catarrhini is the infraorder of the Old World monkeys, apes, and hominids. Along with their geographic distinction, catarrhines can be distinguished from platyrrhines by their narrow nose shape, fewer premolar teeth, and lack of a prehensile tail.

Cercopithecidae (*sir-co-pih-thee'-sih-day*) The family that includes all the Old World monkeys.

Cercopithecoidea (*sir-co-pith-ah-coy'-dee-ah*) The superfamily of all monkeys of Europe, Africa, and Asia.

Eosimiidae (*ee-oh-sim-ee'-ih-day*) A group of early primates from Asia, dated at around 45 mya, that may represent direct ancestors of monkeys, apes, and hominids.

Gigantopithecus **(*ji-gan-tow-pith'-ah-cuss*)** A genus of fossil apes, dated at 7 mya to perhaps as recently as 300,000 ya, found in China, India, and Vietnam. It may have reached a height of 12 feet when standing erect and weighed 1,200 pounds, making it the largest primate known.

Gorilla gorilla **(*guh-ril'-ah guh-ril'-ah*)** The gorilla (well, duh!), one of the three great ape species from Africa and the largest living primate.

Gorillinae (*guh-ril'-ih-nay*) In a cladistic taxonomy, the subfamily for the gorilla, as distinct from Hominidae, the subfamily for humans, chimps, and bonobos.

Haplorhini (*hap-low-rine'-eye*) According to the cladistic taxonomic system, one of two suborders of order Primates (the other is Strepsirhini). Haplorhini are primates lacking a moist nose and other primitive features. Includes the tarsier and all primates traditionally included in suborder Anthropoidea.

Hominidae (*ho-mih'-nih-day*) In a traditional taxonomy, the family of modern and extinct human species, defined as the primates that are habitually bipedal. Members of this group are called hominids.

Homininae (*ho-mih'-nih-nay*) In a cladistic taxonomy, a subfamily that includes chimpanzees, bonobos, and humans. (In such a taxonomy, Hominidae would include the African great apes and humans.)

Hominini (*ho-mih-nih'-nee*) In a cladistic taxonomy, the tribe for humans.

Hominoidea (*ho-min-oy'-dee-ah*) The superfamily that includes the large, tailless primates: apes and hominids, living and extinct.

Homo antecessor **(*ho'-mow an-tee-sess'-or*)** A recently proposed species from Spain dated at 1 to 2 mya. The fossils show a mix of primitive and modern human features and are interpreted by their discoverers as possibly ancestral to *H. heidelbergensis* and *H. neanderthalensis*. This species is not widely recognized at present.

Homo erectus **(*ho'-mow ee-reck'-tuss*)** A fossil hominid species dating from at least 1.8 mya to 100,000 ya or so. First appearing in Africa, *H. erectus* was the first hominid species to expand beyond that continent. Fossils are found throughout Africa and Asia, and there is possible evidence in Europe. Members of this species, with an average brain size about two-thirds that of modern humans, made advances in stone-tool technology and were able to control fire late in their existence.

Homo ergaster **(*ho'-mow er-gas'-ter*)** The earliest *H. erectus* fossils from Kenya, said by some researchers to be sufficiently different that they represent a separate species that was ancestral to both *H. erectus* and, later, *H. sapiens*.

Homo floresiensis **(*ho'-mow floor-ee-see-en'-sis*)** Proposed species from Flores Island, Indonesia, dated at 74,000 to 12,000 ya and noteworthy for having brain and body sizes of the australopithecines. This taxon is still controversial.

Homo habilis **(*ho'-mow hah'-bill-us*)** Fossil hominid species dating from about 2.3 to 1.44 mya and found in East Africa and perhaps southern Africa. Fully bipedal and with an average brain size of 680 ml, *H. habilis* was the first confirmed hominid stone toolmaker. Because this was the first hominid with a brain larger than that of a chimpanzee, and because of the species' associa-tion with stone tools, *H. habilis* is thought to be the earliest member of our genus, *Homo*.

Homo heidelbergensis **(*ho'-mow high-del-berg-en'-sis*)** A proposed species from Africa, Asia, and Europe, dated at between 475,000 and 200,000 ya. They had a modern-human brain size but retained primitive features such as brow ridges, prognathism, and postorbital constriction.

Homo neanderthalensis **(*ho'-mow nee-an-dir-tall-en'-sis*)** A proposed species from Europe and Southwest Asia, dated at between 225,000 and 28,000 ya. They had more pronounced versions of some of the cranial features of *H. heidelbergensis*, such as brow ridges and prognathism. The postcranial skeletons were robust and heavy, with short arms and legs, possibly adaptations to cold climates.

Homo rudolfensis **(*ho'-mow rue-dolf-en'-sis*)** Thought by some authorities to be a separate species made up of the East Turkana, Kenya, specimens traditionally placed in *H. habilis*.

Homo sapiens **(*ho'-mow say'-pee-ens*)** The taxonomic name for modern humans. There is debate as to whether this name covers certain other species, including *H. erectus, ergaster, antecessor, heidelbergensis*, and *neanderthalensis*.

Hylobatidae (*high-low-bat'-ah-day*) The family that includes the gibbons and siamangs, the arboreal so-called lesser apes of Southeast Asia. They are highly efficient brachiators.

Kenyanthropus platyops (*ken-yan'-throw-pus plat'-ee-ops*) A new fossil genus from Kenya, dated at 3.5 mya and suggested by some authorities, because of its flat face and other features, to represent a better human ancestor than any species of *Australopithecus*. Thus far, it is based on only two specimens.

Kenyapithecus (*ken-ya-pith'-ah-cuss*) A fossil genus from East Africa dated at 14 mya. A possible candidate for the first hominoid.

Omomyidae (*oh-mow-me'-ah-day*) A group of early primates that lived in the previously connected landmass of North America and Europe. Dating to more than 50 mya, they are thought to be ancestral to tarsiers and may have been ancestral to Anthropoidea.

Orrorin tugenensis (*or-or'-in too-gen-en'-sis*) A new fossil genus from Kenya, based on thirteen specimens and dated at 6.2 to 5.6 mya. Its purported bipedal features have led some to suggest it represents the ancestor of all later hominids. The identity and features of this form are still a matter of much debate.

Ouranopithecus (*oo-ran-oh-pith'-ah-cuss*) An ape from Greece dated at 10 to 9 mya. Based on some hominid-like features, it is thought by some to be a member of the ape line that led to the hominids.

Panini (*pan'-ih-nee*) In a cladistic taxonomy, the tribe that includes chimpanzees and bonobos.

Pan paniscus (*pan pan-iss'-cuss*) The bonobo, sometimes called the pygmy chimpanzee. One of the three great ape species from Africa.

Pan troglodytes (*pan trog-low-dye'-tees*) The chimpanzee. One of the three great ape species from Africa.

Papio (*pah'-pee-oh*) A genus within superfamily Cercopithecoidea (the Old World monkeys) that comprises several species of baboons, large monkeys living in social groups on the African savannas.

Paranthropus aethiopicus (*par-an'-throw-puss ee-thee-oh'-pih-cuss*) A species from East Africa dating from 2.8 to 2.2 mya. They were the first members of the so-called robust early hominids, having large, rugged features associated with chewing; although other features, including their brain size, were very similar to those of genus *Australopithecus*. Many authorities still include it in that genus. It is thought they were adapted to tough, gritty, hard vegetable foods. The most famous, and first, specimen of this species was the "Black Skull."

Paranthropus boisei (*par-an'-throw-puss boys'-ee-eye*) The East African robust hominid, dated at 2.2 to 1 mya. It had large features associated with chewing, although less pronounced than in *P. aethiopicus*. The first specimen was "Zinjanthropus." Sometimes included in genus *Australopithecus*.

Paranthropus robustus (*par-an'-throw-puss row-bus'-tus*) The southern African robust hominid, dated at 2.2 to 1.5 mya. Although noteworthy for their robust chewing features, this trait was less robust than in either *P. aethiopicus* or *P. boisei*. The postcranial skeleton and the brain size remained similar to those of *Australopithecus*. It is sometimes included in that genus.

Platyrrhini (*plat-ee-rine'-eye*) One of two infraorders of suborder Anthropoidea (the other is infraorder Catarrhini, the Old World monkeys, apes, and hominids). Platyrrhines comprise the New World monkeys. Members of this group can be told apart from the catarrhines by their broad nose shape, greater number of premolar teeth, and the fact that several species have prehensile tails.

Plesiadapiformes (*pleez-ee-ah-dah'-pih-form-ees*) A branch of archaic primates from sites in presentday North America that became extinct about 55 mya.

Pongidae (*pon'-jih-day*) In a traditional taxonomy, the family of the great apes: the orangutans of Southeast Asia and the gorillas, chimpanzees, and bonobos of Africa. In a cladistic taxonomy, the family of the orangutans only.

Pongo pygmaeus (*pon'-go pig-may'-us*) The orangutan. The only great ape from Southeast Asia.

Primates (*pry-mate'-ees*) An order within class Mammalia. Large-brained arboreal mammals with stereoscopic color vision and grasping hands (and sometimes feet). Includes prosimians, monkeys, apes, and hominids.

Prosimii (*pro-sim'-ee-eye*) According to the traditional taxonomic system, one of two suborders of order Primates (the other suborder is Anthropoidea). Prosimians are the more primitive of the two suborders in that they retain features of some of the oldest primate fossils. Many lack color vision, are nocturnal, and have limited opposability of the thumb.

Sahelanthropus tchadensis (*sah-hale-an'-throw-puss chad-en'-sis*) A possible fossil hominid from Chad, dated at 7 to 6 mya. Despite some apelike features, it has other cranial features that some claim make it the earliest hominid.

Sivapithecus (*she-vah-pith'-ah-cuss*) Genus of fossil ape from India and Pakistan, dated at 15 to 12 mya. Thought to be ancestral to the orangutan.

Strepsirhini (*strep-sir-rine'-eye*) According to the cladistic taxonomic system, one of two suborders of order Primates (the other is Haplorhini). These primates have a moist nose and other primitive features. Includes all primates traditionally in suborder Pro-simii except the tarsier.

GLOSSARY OF TERMS

absolute dating technique A dating method that gives a specific age, year, or range of years for an object or site. Compare with **relative dating technique.**

Acheulian technique A toolmaking tradition associated with *Homo erectus* in Africa and Europe. Includes hand axes, cleavers, and flake tools.

adaptation The state in which an organism is adjusted to and can survive in its environment through its physical traits and behaviors. Also, the process by which an organism develops this state through natural processes.

adaptive radiation The evolution and spreading out of related species into new niches.

allele frequency The percentage of times a particular allele appears in a population. Another name, and the preferred term, for gene frequency.

alleles Variants of a gene. Most genes possess more than one possible allele, the different alleles conveying different instructions for the development of a certain phenotype (for example, different blood types).

amino acids The chief components of proteins. Each "word" in the genetic code stands for a specific amino acid.

anthropology The biocultural study of the human species. Anthropology includes the study of human biology, human physical evolution, human cultural evolution, and human adaptation.

antibodies Proteins in the immune system that react to foreign antigens.

antigens Substances, such as proteins, that can trigger an immune response, for example, the production of an antibody. The antigens of the ABO blood-group system are examples.

applied anthropology Anthropology used to address current practical problems and concerns.

arboreal Adapted to life in the trees.

archaeology A subfield of anthropology that studies the human cultural past and the reconstruction of past cultural systems.

argon/argon dating A radiometric dating technique that measures the rate of decay of radioactive argon into stable argon gas. Can be used to date smaller samples and volcanic rock with greater accuracy than potassium/argon dating. See also **potassium/argon dating.**

asexually Reproducing without sex, by fissioning or budding. Compare with **sexually.**

bifacial A stone tool that has been worked on both sides.

bioanthropology Another name for **biological anthropology.**

biocultural Focusing on the interaction of biology and culture.

biological anthropology A subfield of anthropology that studies humans as a biocultural species.

biostratigraphy The study of fossils in their stratigraphic context. Used as a relative dating technique.

bipedal Walking on two legs.

bottleneck A severe reduction in the size of a population or the founding of a new population by a small percentage of the parent population that results in only some genes surviving and characterizing the descendant population.

brachiation Locomotion by swinging arm-over-arm.

breeding populations Populations within a species that are genetically isolated to some degree from other populations.

carnivore An organism adapted to a diet of mostly meat. Compare with **omnivore.**

catastrophists Those who believe that the history of the earth is explained by a series of global catastrophes, either natural or divine in origin. See also **uniformitarianism.**

chromosomal mutations Mutations of a whole chromosome or a large portion of a chromosome. Compare with **point mutations.**

chromosomes Strands of DNA in the nucleus of a cell.

cladistic A classification system based on order of evolutionary branching rather than on present similarities and differences. Compare with **phenetic taxonomy.**

cline A geographic continuum in the variation of a particular trait.

codominant When both alleles of a pair are expressed in the phenotype.

codon The three-base sequence that codes for a specific amino acid. Technically, the sequence on the mRNA.

competitive exclusion What occurs when one species outcompetes others for the resources of a particular area.

core tools Tools made by taking flakes off a stone nucleus. See also **flake tools.**

cultural anthropology A subfield of anthropology that focuses on human cultural behavior and cultural systems and the variation in cultural expression among human groups.

culture Ideas and behaviors that are learned and shared. Also, the system made up of the sum total of these ideas and behaviors that is unique to a particular society of people. Nonbiological means of adaptation.

deduction Suggesting specific data that would be found if a hypothesis were true, a step in the scientific method involving the testing of hypotheses. See also **induction.**

deoxyribonucleic acid (DNA) The molecule that carries the genetic code.

diurnal Active during the day. Compare with **nocturnal.**

DNA See **deoxyribonucleic acid.**

dominance hierarchy A social pattern among animal species where there are recognized individual differences in power, influence, and access to resources and mating. Found in many primate species.

dominant The allele of a heterozygous pair that is expressed in the phenotype. Compare with **recessive.**

ecotone An area where two ecosystems overlap or grade into one another.

endocasts Natural or human-made casts of the inside of a skull. The cast reflects the surface of the brain and allows us to study the brains of even extinct species.

endogamy Restricting marriage to members of the same culturally defined group.

environmental Any nongenetic influence on the phenotype. Also refers to the conditions under which an organism exists, such as climate, altitude, other species, food sources, and so on.

enzymes Proteins that control chemical processes.

epidemiological Pertaining to the study of disease outbreaks and epidemics.

estrus The period of female fertility or the signals indicating this condition.

ethology The study of the natural behavior of animals under natural conditions.

evolution Change through time, usually with reference to biological species, but may also refer to changes within cultural systems.

fission A process of evolution that involves the splitting up of a population to form new populations.

fitness The relative adaptiveness of an individual organism, measured ultimately by reproductive success.

flake tools Tools made from the flakes removed from a stone core. See also **core tools.**

folk taxonomies Cultural categories for important items and ideas. Gender and race are examples of folk taxonomies.

foramen magnum The hole in the base of the skull through which the spinal cord emerges and around the outside of which the top vertebra articulates.

fossils Remains of life-forms of the past.

founder effect A process of evolution. Genetic differences between populations produced by the fact that genetically different individuals established (founded) those populations.

gametes The cells of sexual reproduction, commonly sperm and egg, which contain only half the chromosomes of a normal cell.

gamete sampling A process of evolution. The genetic change caused when genes are passed to new generations in percentages unrepresentative of those of the parental generation. An example of **sampling error.**

gender The cultural categories and characteristics of men and women. The translation of sex into a folk taxonomy. Compare with **sex.**

gene flow A process of evolution that involves the exchange of genes among populations through interbreeding.

gene frequency See **allele frequency.**

gene pool All the alleles in a population.

generalized Species that are adapted to a wide range of environmental niches. Such species tend to be genetically and physically variable. Compare with **specialized.**

genes Those portions of the DNA molecule that code for a functional product, usually a protein.

genome The total genetic endowment of an organism.

genotypes The alleles possessed by an organism. See also **phenotype.**

glaciers Massive sheets of ice that expand and move. Found on the polar ice caps and in mountains.

grooming Cleaning the fur of another animal, which promotes social cohesion. Common among primate groups.

haft To attach a wooden handle or shaft to a stone or bone point.

half-life The time needed for one-half of a given amount of a radioactive substance to decay.

hand axe A bifacial, all-purpose stone tool, shaped somewhat like an axe head. First invented by *Homo erectus* and usually associated with that species.

haplotype A combination of particular expressions of **SNPs** along a chromosome or stretch of DNA. This may show regional patterns of variation.

heterozygous Having two different alleles in a gene pair. Compare with **homozygous.**

holistic Assuming an interrelationship among the parts of a subject. Anthropology is a holistic discipline.

homozygous Having two of the same allele in a gene pair. Compare with **heterozygous.**

human ecology A specialty of anthropology that studies the relationships between humans and their environments.

hypotheses Educated guesses to explain natural phenomena. In the scientific method, hypotheses must be testable. See also **theory.**

induction Developing a general explanation from specific observations. The step in the scientific method that generates hypotheses. See also **deduction.**

inheritance of acquired characteristics The incorrect idea, associated with Lamarck, that adaptive traits acquired during an organism's lifetime can be passed on to its offspring.

intelligence The relative ability of the brain to acquire, store, retrieve, and process information.

intelligent design The idea that an intelligent designer played a role in some aspect of the evolution of life on earth, usually the origin of life itself. Generally, a thinly disguised version of **scientific creationism.**

Levallois technique A tool technology involving striking uniform flakes from a prepared core. See **core tools** and **flake tools.**

linguistic anthropology A subfield of anthropology that studies language as a human characteristic and attempts to explain the differences among languages and the relationship between a language and the society that uses it.

macroevolution The branching of new species from existing species.

macromutations Mutations with extensive and important phenotypic results. The mutations for sickle cell anemia and Down syndrome are examples.

meiosis The process of cell division in which gametes are produced, each gamete having one-half the normal complement of chromosomes and, therefore, only one allele of each original pair. See also **mitosis.**

melanin The pigment largely responsible for human skin color.

melanocytes Specialized skin cells that produce the pigment melanin.

Mendelian genetics The basic laws of inheritance discovered by Gregor Mendel in the nineteenth century.

messenger ribonucleic acid (mRNA) The molecule that carries the genetic code out of the nucleus for translation into proteins. See also **transfer RNA.**

microevolution Evolutionary change within a single species through time.

mitochondrial DNA (mtDNA) The genetic material found in the cell's mitochondria rather than in the cell's nucleus. The mtDNA does not play a role in inheritance and thus may give a more accurate measure of the genetic differences among populations.

mitosis The process of cell division that results in two exact copies of the original cell. See also **meiosis.**

monogenic A trait coded for by a single gene. The ABO blood-group system is a monogenic trait. Compare with **polygenic.**

Mousterian technique A toolmaking tradition associated with the European Neandertals.

mutation Any mistake in an organism's genetic code.

natural selection Evolutionary change based on the differential reproductive success of individuals within a species.

nocturnal Active at night. Compare with **diurnal.**

Oldowan A toolmaking tradition from Africa associated with early *Homo*.

omnivore An organism with a mixed diet of animal and vegetable foods. Compare with **carnivore.**

opposability The ability to touch (oppose) the thumb to the tips of the other fingers on the same hand.

organic Molecules that are part of living organisms. They are based on the chemistry of carbon and contain mostly hydrogen, oxygen, carbon, and nitrogen. Even carbon-based molecules that are not found in living things are sometimes referred to as organic. Compare with **inorganic.**

osteology The study of the structure, function, and evolution of the skeleton.

paleoanthropology A specialty that studies the human fossil record.

paleopathology The study of disease and nutritional deficiency in prehistoric populations, usually through the examination of skeletal material.

Pangea The supercontinent that included parts of all present-day landmasses. It formed around 280 mya and began breaking up around 200 mya.

particulate The idea that biological traits are controlled by individual factors rather than by a single all-encompassing hereditary agent.

petrified Turned to stone. As the organic material of a fossil decays, it is slowly replaced by minerals, leaving a cast in stone of the organism or some of its parts.

phenetic taxonomy A classification system based on existing phenotypic features and adaptations. Compare with **cladistic.**

phenotype The chemical or physical results of the genetic code. See also **genotypes.**

photosynthesis The process by which plants manufacture their own nutrients from carbon dioxide and water, using chlorophyll as a catalyst and sunlight as an energy source.

physical anthropology The traditional name for **biological anthropology.**

plate tectonics The movement of the plates of the earth's crust, caused by their interaction with the molten rock of the earth's interior. The cause of continental drift.

Pleistocene The geological time period, from 1.6 mya to 10,000 ya, characterized by a series of glacial advances and retreats. See **glaciers.**

point mutations Mutations of a single base of a codon. The mutation that causes sickle cell anemia is an example. Compare with **chromosomal mutations.**

polygenic A trait coded for by more than one gene. Skin color is a polygenic trait. Compare with **monogenic.**

postnatal dependency The period after birth during which offspring require the care of adults to survive.

postorbital constriction A narrowing of the skull behind the eyes, as viewed from above.

potassium/argon (K/Ar) dating A radiometric dating technique measuring the rate at which radioactive potassium, found in volcanic rock, decays into stable argon gas. See also **argon/argon dating.**

prehensile Having the ability to grasp.

primates Large-brained, mostly tree-dwelling mammals with three-dimensional color vision and grasping hands. Humans are primates.

primatology A specialty of anthropology that studies nonhuman primates.

prognathism The jutting forward of the lower face and jaw area.

progressive In evolution, the now-discounted idea that all change is toward increasing complexity.

prosimian A primate with primitive features most closely resembling the ancient primates.

proteins Molecules that make cells and carry out cellular functions. Proteins are made of amino acids.

protein synthesis The process by which the genetic code puts together proteins in the cell.

provenience The precise location where a fossil or an artifact was found.

pseudoscience Scientifically testable ideas that are taken on faith, even if tested and shown to be false. Scientific creationism is a pseudoscience.

punctuated equilibrium The view that species tend to remain stable and that evolutionary changes occur fairly suddenly through the evolution of new species branching from existing ones.

quadrupedal Walking on all four limbs.

races In biology, the same as subspecies. In culture, cultural categories to classify and account for human diversity; see **folk tax-onomies.**

racism Judging an individual based solely on his or her racial affiliation.

radiocarbon dating A radiometric dating technique measuring the decay rate of a radioactive form of carbon found in organic remains.

radiometric Referring to the decay rate of a radioactive substance. See **argon/argon dating; radiocarbon dating;** and **potassium/argon dating.**

recessive The allele of a heterozygous pair that is not expressed. For a recessive allele to be expressed, it must be homozygous. Compare with **dominant.**

reification Translating a complex set of phenomena into a single entity such as a number. IQ testing is an example.

relative dating technique A dating method that indicates the age of one item in comparison to another. Stratigraphy provides relative dates by indicating that one layer is older or younger than another. Compare with **absolute dating technique.**

replication The copying of the genetic code during cell division.

reproductive isolating mechanism Any difference that prevents the production of fertile offspring between members of two populations. Necessary for the production of separate species.

RNA See **messenger RNA** and **transfer RNA.**

sagittal crest A ridge of bone, running from front to back along the top of the skull, for the attachment of chewing muscles.

sagittal keel A sloping of the sides of the skull toward the top, as viewed from the front.

sampling error When a sample chosen for study does not accurately represent the population from which the sample was taken. See **gamete sampling.**

savanna The open grasslands of the tropics. The savannas of Africa are important in early hominid evolution.

science The method of inquiry that requires the generation, testing, and acceptance or rejection of hypotheses.

scientific creationism The belief in a literal biblical interpretation regarding the creation of the universe, with the connected belief that this view is supported by scientific evidence. An example of a pseudoscience.

scientific method The process of conducting scientific inquiry. See **science.**

segregation In genetics, the breaking up of allele pairs in the production of gametes.

sex The biological categories and characteristics of males and females. Compare with **gender.**

sexual dimorphism Physical differences between the sexes of a species that are not related to reproductive features. See **sex.**

sexually Reproducing by combining genetic material from two individuals. Compare with **asexually.**

single nucleotide polymorphism (SNP) A single base pair of the genetic code that displays variable expressions among individuals.

sites Locations that contain fossil and archaeological evidence of human presence.

specialized Species that are adapted to a narrow range of environmental niches. Compare with **generalized.**

speciation The evolution of new species.

species A group of organisms that can produce fertile offspring among themselves but not with members of other groups. A closed genetic population, usually physically distinguishable from other populations.

stereoscopic vision Three-dimensional vision; depth perception.

strata Layers; here, the layers of rock and soil under the earth's surface. Singular, *stratum.*

stratigraphy The study of the earth's strata.

subspecies Physically distinguishable populations within a species. See **races.**

superposition The principle of stratigraphy that, barring disturbances, more recent layers are superimposed over older ones.

symbiosis An adaptive relationship between two different species, often, but not necessarily, of mutual benefit.

symbolic A communication system that uses arbitrary but agreed-upon sounds and signs for meaning.

taphonomy The study of how organisms become part of the paleontological record—how fossils form and what processes affect them through time.

taxa Categories within a taxonomic classification; singular, *taxon.* See **taxonomy.**

taxonomists Scientists who classify and name living organisms.

taxonomy A classification based on similarities and differences. In biology, the science of categorizing organisms and of naming them so as to reflect their relationships. See **cladistic** and **phenetic taxonomy.**

theory A well-supported general idea that explains a large set of factual patterns. In science, theory is a positive term.

torus A bony ridge at the back of the skull, where the neck muscles attach.

transcription The process during which mRNA is formed from the DNA code.

transfer ribonucleic acid (tRNA) RNA that lines up amino acids along mRNA to make proteins. See also **messenger RNA.**

translation The process during which the mRNA code builds a protein using amino acids supplied by tRNA.

trephination Cutting a hole in the skull, presumably to treat some illness, a practice of some societies with prescientific knowledge.

tundra A treeless area with low-growing vegetation and permanently frozen ground. Located in the Arctic today, tundras were found during the Pleistocene in the vicinity of glaciers far to the south.

uniformitarianism The idea that present-day geological and biological processes can also explain the history of the earth and its life. See also **catastrophists.**

vertebrates Organisms with backbones and internal skeletons.

zygote The fertilized egg before cell division begins.

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